

DIVERSITY AND STABILITY OF BIRD COMMUNITIES IN TURKIYE AND
EUROPE

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ABSTRACT

DIVERSITY AND STABILITY OF BIRD COMMUNITIES IN TURKIYE AND EUROPE

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Biodiversity is essential for functioning of ecosystems and human existence. However, human activities have driven an unparalleled loss of biodiversity globally. Despite their ecological importance, birds are among the most impacted organisms, with 12% of all species facing extinction. In this thesis, I adopted a trait-based approach and used breeding bird atlases alongside generalized linear mixed-effect and spatial error models to examine (i) how extensive wetland degradation in central Türkiye has altered diversity of breeding wetland bird communities across spatial scales (ii) the extrinsic and intrinsic factors driving the temporal stability of breeding bird communities in Europe. Results showed that the decline in functional diversity of wetland birds in central Türkiye was stronger than taxonomic declines, with widespread species losses making communities taxonomically and functionally more heterogenous in space. Additionally, advancing seasonal shrinking/drying of wetlands likely threatens late-breeding endangered wetland birds in the region. Analyses concerning the community stability of European breeding bird communities revealed that extrinsic factors such as mean elevation, proportion of protected areas, biome coverage, and climate change significantly influenced taxonomic and functional stability. Communities with taxonomically or functionally

similar neighbors remained more stable. Several intrinsic factors, including species richness and specific aspects of functional diversity, including redundancy, were also significantly associated community stability. The findings presented in this thesis can help guide conservation efforts, provide insight into the factors shaping stability of bird communities, and establish a foundation for future studies aiming at predicting vulnerability of communities to compositional and functional changes.

Keywords: Biodiversity, Climate change, Community stability, Functional diversity, Wetland birds



ÖZ

TÜRKİYE VE AVRUPA'DAKİ KUŞ KOMÜNİTELERİNİN ÇEŞİTLİLİĞİ VE STABİLİTESİ

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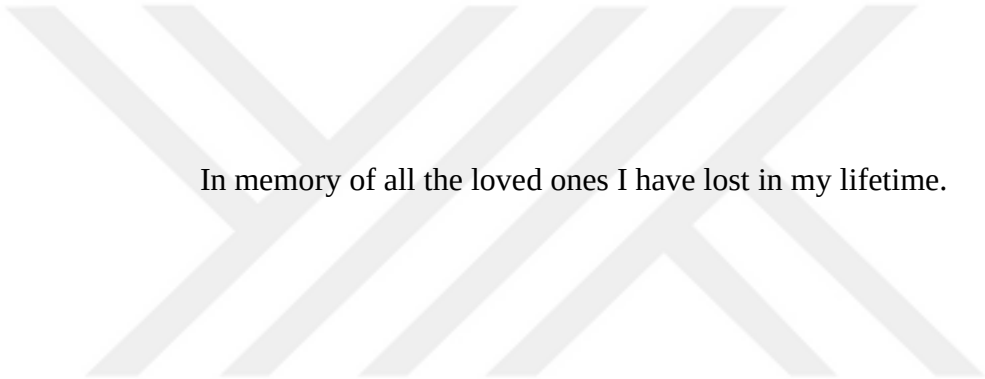
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Biyçeşitlilik, ekosistemlerin işleyişi ve insan varlığı için hayati öneme sahiptir. Ancak, insan faaliyetleri küresel ölçekte eşi görülmemiş bir biyçeşitlilik kaybına neden olmaktadır. Kuşlar, ekolojik önemlerine rağmen en fazla etkilenen organizmalar arasındadır ve tüm kuş türlerinin %12'si yok olma tehlikesi altındadır. Bu tezde, fonksiyonel bir yaklaşım benimseyerek, üreyen kuş atlaslarını, genelleştirilmiş lineer karma-etki ve mekânsal hata modelleri ile birlikte kullanarak (i) Türkiye'nin iç kesimlerindeki yaygın sulak alan tahribatının üreyen sulak alan kuş topluluklarının çeşitliliği üzerindeki farklı mekânsal ölçeklerde etkilerini, (ii) Avrupa'daki üreyen kuş komünitelerinin zamansal stabilitesini belirleyen dışsal ve içsel faktörleri inceledim. Sonuçlar, Türkiye'nin iç kesimlerindeki sulak alan kuşlarının işlevsel çeşitliliğindeki azalmanın taksonomik düşüşlerden daha güçlü olduğunu ve yaygın tür kayıplarının komüniteleri mekânsal olarak daha heterojen hale getirdiğini gösterdi. Ayrıca, sulak alanların mevsimsel olarak daha erken kurumasının, geç üreyen tehlike altındaki sulak alan kuşlarını tehdit ediyor olabileceği tespit edildi. Avrupa'daki üreyen kuş topluluklarının stabilitesi üzerine yapılan analizler, ortalama yükselti, korunan alan oranı, biyom kapsamı ve iklim değişikliğinin taksonomik ve fonksiyonel stabiliteyi önemli ölçüde etkilediğini

ortaya koydu. Taksonomik veya fonksiyonel olarak benzer komşulara sahip komüniteler daha stabil kaldı. Tür zenginliği ve belirli fonksiyonel çeşitlilik bileşenleri gibi bazı içsel faktörlerin de topluluk stabilitesinin ile önemli ölçüde ilişkili olduğu bulundu. Bu tezde sunulan bulgular, koruma çalışmalarına rehberlik edebilir, kuş komünitelerinin stabilitesini şekillendiren faktörlere dair fikir sağlayabilir ve komüniteleri kompozisyonel ve fonksiyonel değişimlere karşı hassasiyetini tahmin etmeye yönelik gelecekteki çalışmalar için bir temel oluşturabilir.

Anahtar Kelimeler: Biyoçeşitlilik, Fonksiyonel çeşitlilik, İklim değişikliği, Komünite stabilitesi, Sulak alan kuşları



In memory of all the loved ones I have lost in my lifetime.

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LIST OF ABBREVIATIONS

ABBREVIATIONS

AIC: Akaike Information Criterion.

AT: Regional atlas data

AUC: Area under the curve

CAS: Casual observations

CCI: Climate Change Initiative

CI: Confidence interval

CWM: Community weighted mean

DR: Direct observation.

EBBA1: European Breeding Bird Atlas 1

EBBA2: European Breeding Bird Atlas 2

EBCC: European Bird Census Council

ESA: European Space Agency.

FDiv: Functional divergence.

FDis: Functional dispersion.

FEve: Functional evenness.

FIde: Functional identity.

FMPD: Functional mean pairwise distance.

FRed: Functional redundancy.

FOri: Functional originality.

FRic: Functional richness.

FSpe: Functional specialization.

FNND: Functional nearest neighbor distance.

$F_{\beta_{SIM}}$: Functional turnover.

$F_{\beta_{SNE}}$: Functional nestedness.

$F_{\beta_{SOR}}$: Total functional Sørensen dissimilarity.

GBIF: Global Biodiversity Information Facility

GLM: Generalized linear model.

HFPI: Human Footprint Index.

HWI: Hand-Wing Index.

IBA: Important Bird Area.

IPCC: Intergovernmental Panel on Climate Change.

IUCN: International Union for Conservation of Nature.

KCB: Konya Closed Basin.

KNN: k -nearest neighbor.

LC: Land cover.

LR: Local records.

MAE: Mean absolute error.

Mad: Mean absolute deviation.

m.a.s.l.: Meters above the sea level.

m.b.s.l.: Meters below the sea level.

MNDWI: Modified normalized difference water index.

MON: Monitoring data.

OLS: Ordinary least squares.

PCA: Principal component analysis.

PCoA: Principal coordinate analysis

Q-Q plot: Quantile-quantile plot.

RMSE: Root mean square error.

SAC: Spatial autocorrelation.

SAR: Simultaneous autoregressive model.

SEM: Spatial error model.

SL: Length of the secondary wing feather.

TAR: Targeted surveys.

VIF: Variance inflation factor.

VR: Visitor records.

WL: Wing length

β_{SOR} : Taxonomic turnover.

β_{SOR} : Taxonomic nestedness.

β_{SOR} : Total taxonomic Sørensen dissimilarity.



CHAPTER 1

CHANGES IN DIVERSITY OF WETLAND BIRDS ACROSS SPATIAL SCALES FOLLOWING 20 YEARS OF WETLAND DEGRADATION IN KONYA CLOSED BASIN TÜRKİYE

In this chapter, me and my colleagues utilized two breeding bird atlases and remote sensing to discover how breeding wetland bird community diversity and wetland drying/shrinking phenology changed following two decades of wetland degradation and loss. This chapter is the product of a collective work I carried out with the help of several other researchers, although I carried out most of the work. The chapter has been submitted as a research article to a journal and it is under review at the time of thesis defense. See section 1.5 for author contributions.

1.1 Introduction

1.1.1 Background

Wetlands play important roles in providing key ecosystem services, including carbon capture, climate stabilization, groundwater recharge, water purification, nutrient cycling, food and raw material provision, and various cultural services (Mitsch et al. 2015), as well as representing habitat for a variety of organisms. Despite their importance, wetlands have been heavily degraded, drained, and modified worldwide as a result of anthropogenic activities (Green et al. 2017). Endorheic basins, defined as closed basins that have internal drainage and no connection to open seas or oceans (Nichols 2011), are particularly vulnerable. They receive limited precipitation and have high potential evapotranspiration; hence, they have fragile water budgets and are highly vulnerable to climate change and human actions such as damming, groundwater extraction, and diversion (Wang et al., 2018). Despite representing only

one-fifth of the world's surface, they represent half of the world's water-stressed regions (Wang et al., 2018). Recent studies have demonstrated that climate change and human actions in some temperate/semi-arid closed basins in the Mediterranean region, where evapotranspiration is predicted to increase and precipitation to decrease (Guillemain et al. 2013), have already led to observable perturbations in water balance (Yılmaz et al. 2021, Çolak et al. 2022).

Birds inhabiting wetlands, especially waterbirds, play important roles in their ecosystems (Green and Elmberg 2014). They help maintain the diversity of other organisms and disperse their propagules, transport nutrients between terrestrial and aquatic ecosystems, control pests, act as sentinels of disease outbreaks, and provide food and cultural services for people (Green and Elmberg 2014). Unfortunately, climate-driven changes and human activities have negatively affected wetland birds, resulting in widespread population declines and range losses as well as altering their community structure and distribution (Guillemain et al. 2013, Elmberg et al. 2020). In this context, recognizing the scale dependency of the responses is critical because the direction and magnitude of diversity changes can strongly depend on it (Murray et al. 2017, Jarzyna and Jetz 2018, Leroy et al. 2023). Indeed, whether wetland changes involve single versus multiple wetlands at the regional scale will have very different consequences for wetland bird conservation. Therefore, studying changes in diversity patterns not only at local scales (α scale), but also at landscape (β scale) and global or regional scales (γ scale) is necessary to thoroughly understand the consequences of habitat loss on biodiversity (Socolar et al. 2016, Si et al. 2016).

It has long been argued that β diversity can be decomposed in two different and antithetic components: turnover, which accounts for differences due to species replacement among sites, and nestedness, which accounts for differences resulting from poorer assemblages being mostly a subset of richer assemblages (Baselga et al. 2007, Baselga 2010). These two components can be driven by different biotic processes; thus, they should be disentangled to better understand underlying biological processes and guide conservation efforts (Baselga 2010, Soininen et al. 2018). A number of studies have investigated the impact of habitat loss on diversity

of birds inhabiting wetlands, but those studies have selectively focused on waterbirds (e.g., Almeida et al., 2019). However, other wetland birds, such as reed-dwelling passerines and other birds that can use wetlands for different purposes such as foraging, also play important roles in these delicate ecosystems and yet remain understudied.

A vast amount of literature suggests that trait-based approaches relate better with community dynamics, assembly, resilience, stability, and ecosystem functioning and services than the conventional taxonomic approaches (Violle et al. 2007a, Luck et al. 2012, de Bello et al. 2021b). Therefore, quantifying and describing trait diversity within a community can be vital for understanding ecosystem functioning (Cadotte 2017), predicting responses to habitat changes (Teresa and Casatti 2017), and for efficient conservation planning (Cadotte et al. 2011). In this context, functional diversity, which can be defined as the extent of trait differences among species in a community (Villéger et al. 2008a), and has become a valuable tool to understand potential impacts of ecosystem changes on vulnerable ecosystems.

1.1.2 Aims, objectives, and hypotheses

Here, I explored how the timing of the seasonal shrinking/drying of lakes and the taxonomic and functional diversity of all breeding wetland birds at different spatial scales changed following widespread wetland loss and degradation, salinization, and climate change in Konya Closed Basin (KCB) in central Türkiye between 1998 and 2018. Given the increased water extraction and summer temperatures in the region (Yılmaz et al. 2021), I hypothesized that seasonal shrinking and drying of wetlands would advance over the study period. Additionally, I hypothesized, declines in taxonomic and functional diversity at all spatial scales due to widespread extinctions and homogenizations (Leroy et al. 2023), However, I expected the magnitude of these declines to differ, with greater declines in functional diversity due to loss of functionally distinct species and persistence of a small number of generalist species (Liang et al. 2019).

1.2 Material and methods

1.2.1 Study area

The current study focused on KCB in Central Anatolia, Türkiye. With a surface area of approximately 50,000 km² (Figure 1.1), KCB is the largest endorheic basin in the country (Ekercin et al. 2019). Its average altitude is 1,000 m, and the prevailing climate types are cold semi-arid steppe and hot-summer/warm-summer temperate continental according to the Köppen-Geiger Climate Classification Scheme (Öztürk et al. 2017). A recent study showed that, over the last 50 years, the long-term mean temperature in the basin has increased, while annual precipitation in some parts of the basin decreased (Yılmaz et al. 2021). Evaporation appeared to be the major driver for wetlands loss in the early Holocene and during the interglacial periods, and uncontrolled water extraction for irrigation seems to be a major contributor to wetland loss in the recent years (Yılmaz et al., 2021).

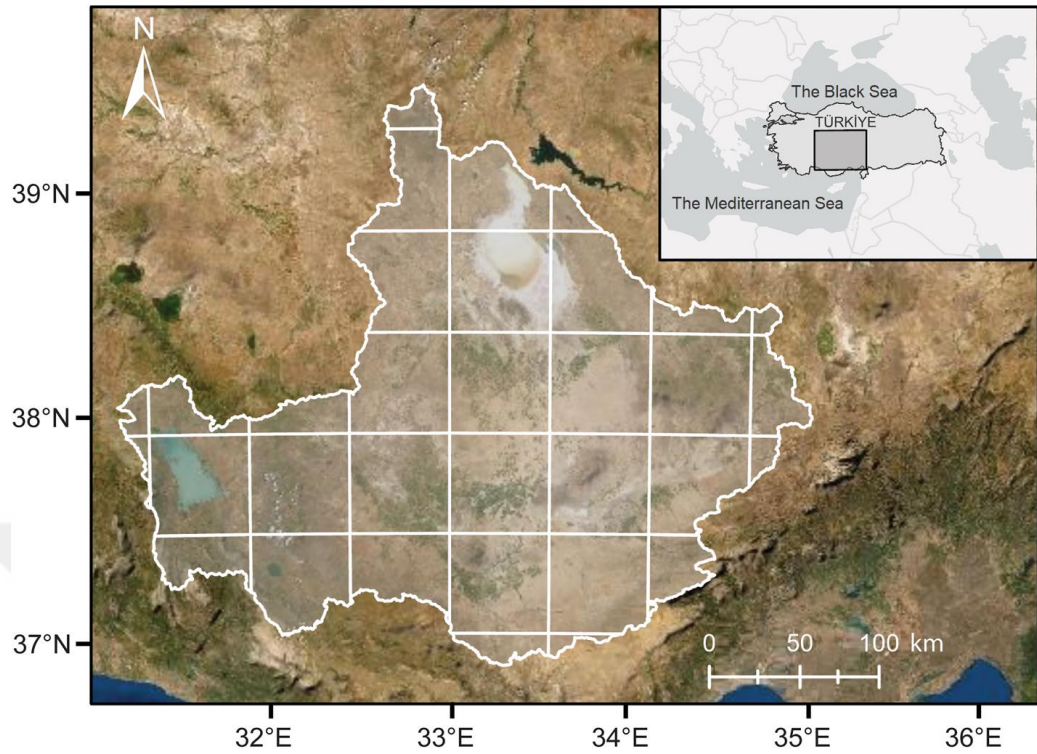


Figure 1.1 Map showing the study area, Konya Closed Basin (KCB). The grid is composed of 50 km x50 km grid cells which are the local study units in the breeding bird atlases.

More than half of the land in KCB is used for crop farming. Although 70% of the total precipitation falls outside the crop growing season, the cultivation of water-intensive crops such as sugar beet (*Beta vulgaris*) has become widespread over the last few decades (Yılmaz et al. 2021). To meet the increasing water demand for irrigation, dam construction and surface or groundwater extraction have become more common, resulting in drainage of lakes and marshes, of which some were as large as 215 km² (Eken et al. 2006, Yılmaz et al. 2021). Long-term remote sensing analyses showed that some of the remaining wetlands have become substantially smaller and more saline over the last 35 years, and that wetland degradation and loss in the basin have accelerated considerably after the early-2000s, coinciding with increases in fertilizer utilization, total irrigated area, and water use. Most of the water used in crop irrigation comes from 22 reservoirs present in the region and from

groundwater, which had its average level declined at a rate of 1 m/year between 1995 and 2015 (Yılmaz et al. 2021).

The KCB counts 16 important bird areas (IBAs) and two Ramsar sites, therefore representing an important site for waterbird populations in the region (Kılıç and Eken 2004, Eken et al. 2006). Over the last 50-60 years, many of the wetland IBAs and Ramsar sites in the region have been either completely lost or deteriorated dramatically due to water extraction and diversion (Kılıç and Eken 2004, Yılmaz et al. 2021). As a result, the number of waterbird species and their abundance have declined significantly. KCB has also been home to five globally threatened waterbird species, whose populations have either declined substantially, or disappeared completely during the last 55 years (Yılmaz et al. 2021). A recent study showed that the largest declines in the number of breeding waterbirds and populations of globally threatened waterbirds occurred in the areas where the former extensive marshes were located (Yılmaz et al. 2021). In some of the lakes, water level decrease has also resulted in the loss of islands acting as refugia and breeding habitats for the waterbirds (Karauz and Kıraç 1999).

1.2.2 Remote sensing

Remote sensing part of this chapter was carried out by one of the authors, Mehmet Arda Çolak. Arda calculated the mean surface area of seven IBA lakes that I chose and are known to be important breeding sites for wetland birds in KCB (Eken & Magnin, 2000; Appendix A.1) in two time periods (1996-1998 and 2016-2018) using satellite images. To compare the surface area changes in the early and late breeding season, he examined satellite imagery from the early breeding season (April or first half of May depending on availability of images) and the late breeding season (July or August). Arda downloaded level-1 products from www.earthexplorer.usgs.gov using Landsat Thematic Mapper for the years before 2013 and Operational Land Imager data for the years after 2013. He utilized an atmospheric correction of the satellite images applying the semi-automatic classification plugin in QGIS

(Congedo, 2020; QGIS Development Team, 2020) and then used the Modified Normalized Water Index (MNDWI; Han-Qiu, 2005) to define water pixels. Mehmet Arda Çolak assigned water indicator pixels when the index values were greater than 0.50 to create a binary image, which was vectorized automatically and used in the lake surface water area calculation. Wetlands in the study area are very shallow, eutrophic, and prone to drying out in summer (Yılmaz et al, 2021). Under such conditions, thresholding using the MNDWI index is expected to involve uncertainties due to the presence of shallow and turbid water (Reis et al. 2017). Xu (2006) observed that the performance of MNDWI decreases in water bodies with shallow and turbid water, and advised against using commonly-used index values near zero and recommended adjusting thresholds based on local reflectance variability. In our study area, threshold values close to zero consistently led to the over-detection of surface water. To address this issue, Mehmet Arda Çolak manually set the threshold at 0.5, based on visual inspection of the classified and original satellite imagery. However, we acknowledge that this may limit the generalizability of our approach to other regions with different environmental conditions, such as varying levels of water turbidity or seasonal fluctuations in water level, which could alter reflectance and classification accuracy.

Although other types of land cover changes can also influence wetland bird distributions, we focused exclusively on wetland area in our study for several reasons: (i) other types of land cover changes are expected to affect wetland bird distributions indirectly by altering their surface area, water level, trophic state, or salinity (ii) our sample size is relatively small, consisting of only 34 data points; and (iii) wetland habitat area is expected to be the primary driver of wetland bird distributions due to the strong dependence of these species on wetlands (Li et al. 2019, Soultan et al. 2022).

1.2.3 Breeding bird atlases and wetland bird communities

Our main sources of data were two breeding bird atlases: one conducted in 1998 in the Konya Closed Basin (Eken and Magnin 2000) and the other one in 2018 at the national scale (Boyla et al. 2019). Both atlases were made by using comparable field methods and reported incidence-only data. The 1998 atlas used a combination of point transects and line transects, while the 2018 atlas used line transects with pauses (which can be considered similar to point transects) along with opportunistic observations, and expert opinion. I used a 50 km x 50 km resolution for the analyses because data were available for both atlases at this scale. This resolution is the standard spatial scale used in various atlas projects, including the European Breeding Bird Atlas projects (Keller et al. 2020). Ultimately, I obtained a total of 34 study units (Figure 1.1). The discussion section 1.4.1 provides a detailed description of the methods used in the atlases, our subsequent data processing, and validation procedures to ensure that the two atlases were comparable.

1.2.4 Taxonomic diversity

I quantified breeding wetland bird species richness at γ , β , and α scales for our study area and years. I considered the γ scale or regional diversity for the whole study area and the α scale diversity at the level of individual 50 km x 50 km grid cells. I calculated pairwise and multisite Sørensen dissimilarities for the communities in 1998 and 2018 (β_{SOR}) to quantify taxonomic β diversity (Magurran and McGill 2011). I partitioned the total taxonomic β diversity into its turnover (β_{SIM}) and nestedness (β_{SNE}) components (Baselga, 2010). This partitioning approach has the potential to allow for a deeper understanding of the nature and causes of ongoing changes and their conservation implications (Soininen et al. 2018). Finally, I calculated the extinction and colonization components of the changes in beta diversity, which allowed us to reveal the individual contributions of extinction and

colonization events to the overall change in taxonomic beta diversity (Tatsumi et al., 2022).

1.2.5 Functional diversity

I used 33 functional traits to quantify the functional diversity of the breeding wetland bird communities (Table 1.1 and Appendix A.3). I chose our traits following the guidelines in Violle et al. (2007) and Luck et al. (2012) to represent a wide array of avian attributes related to ecosystem functions, community processes, and response to environmental changes that took place in our study system (e.g., habitat degradation and climate change). These traits include multiple morphological, life cycle and behavioral characteristics, as well as diet, habitat and phenological traits (Table 1.1). Whenever possible, I used locally-collected data (rather than international datasets) to score the traits in order to increase the accuracy and representativeness of our analyses. I removed traits that were significantly and strongly correlated with others and weighted the reminder traits following Laliberté & Legendre (2010), to avoid over-weighting functions that are represented with multiple traits, prior to functional diversity metric calculations. Further details about the functional are given in Appendix A.3.

Table 1.1 Functional traits used in the chapter, their levels, trait types, variable types, and sources used to score them. Full citations of the references used in the table are included in the references section. See Appendix A.3 for information on ecological relevance of the traits.

<i>Trait</i>	<i>Levels</i>	<i>Trait category</i>	<i>Variable type</i>	<i>Sources</i>
Body mass	NA	Response & effect	Continuous	Dunning (2007); Wilman et al. (2014)
Body length	NA	Response & effect	Continuous	Storchová & Hořák (2018)
Wing length	NA	Response & effect	Continuous	Storchová & Hořák (2018)
Bill length	NA	Effect	Continuous	Storchová & Hořák (2018)
Tarsus length	NA	Response & effect	Continuous	Storchová & Hořák (2018)
Relative brain mass	NA	Response	Continuous	Galván & Møller (2011); Garamszegi et al. (2002) Iwaniuk (2004); Jimenez-Ortega et al. (2020) Minias & Podlaszczuk (2017); Sayol et al. (2020) Sol et al. (2010); Tsuboi et al. (2018)
Sexual dimorphism	NA	Response	Continuous	Storchová & Hořák (2018)
Clutch size	NA	Response	Continuous	Storchová & Hořák (2018)
Broods per year	NA	Response	Continuous	Storchová & Hořák (2018); Kirwan et al. (2008)
Reproductive effort	NA	Response	Continuous	Storchová & Hořák (2018); Kirwan et al. (2008)
Early developmental mode	Altricial Semi-altricial Precocial	Response	Nominal	Storchová & Hořák (2018)
Social behavior during breeding season	Colonial Semi-colonial Solitary	Response	Binary	Storchová & Hořák (2018)
Incubation duration	NA	Response & effect	Continuous	Storchová & Hořák (2018)
Fledgling duration	NA	Response & effect	Continuous	Storchová & Hořák (2018)
Age at first reproduction	NA	Response	Continuous	Palomino et al. (1999); Storchová & Hořák (2018)
Daily activity period	Diurnal Crepuscular Nocturnal	Response & effect	Binary	Pearman et al. (2014)
Daily activity period plasticity	NA	Response	Integer	Pearman et al. (2014)
Generation length	NA	Response & effect	Continuous	BirdLife International (2021)

Table 1.1 (continued)

Diet	Invertebrates, Endothermic vertebrates Ectothermic vertebrates, Fish, Carcass Fruits, Seeds, Vegetative parts of plants	Response & effect	Binary	Wilman et al. (2014)
Diet plasticity	NA	Response	Integer	Wilman et al. (2014)
Foraging substrate/stratum	Water (below surface), Water (around surface) Ground, Understory, Forest (mid-high) Canopy, Aerial, Pelagic	Response & effect	Fuzzy	Wilman et al. (2014)
Foraging substrate/stratum plasticity	NA	Response	Integer	Wilman et al. (2014)
Territoriality	NA	Response & effect	Binary	Storchová & Hořák (2018)
Foraging behavior	Pursuit, Sally, Foliage glean Pounce, Graze, Peck Dig, Overturn, Probe	Response & effect	Binary	Cramp (1977); Pearman et al. (2014)
Foraging behavior plasticity	NA	Response	Integer	Cramp (1977); Pearman et al. (2014)
Migratory strategy	Migrant, Resident	Response & effect	Binary	Cornell Lab of Ornithology (2021); Kirwan et al. (2008)
Egg laying season	First and second half of each month	Response & effect	Binary	Cornell Lab of Ornithology (2021); Cramp (1977) Kirwan et al. (2008)
Egg laying season length/plasticity	NA	Response	Integer	Cornell Lab of Ornithology (2021); Cramp (1977) Kirwan et al. (2008)
Breeding habitat	Woodland, Streams, Shrubland Cultivated land, Grassland, Wetland Urban/Suburban, Montane	Response & effect	Binary	Cramp (1977); Kear (2005); Kirwan et al. (2008) Pearman et al. (2014)
Breeding habitat plasticity	NA	Response	Integer	Cramp (1977); Kear (2005); Kirwan et al. (2008) Pearman et al. (2014)
Nesting substrate/stratum	Ground open, Ground hole, Tree open Tree hole, Reeds, Artificial surfaces, Sand banks Shrub, Island, Herbaceous, Cliffs and rocky outcrops Floating vegetation, Brood parasite	Response & effect	Binary	Cramp (1977); Kear (2005); Kirwan et al. (2008) Pearman et al. (2014)
Nesting substrate/stratum plasticity	NA	Response	Integer	Cramp (1977); Kear (2005); Kirwan et al. (2008) Pearman et al. (2014)

I calculated functional richness (FRic; Villéger et al., 2008), which measures the amount of trait space occupied by all species in a community, to quantify the functional diversity of communities at γ , β , and α scales. FRic is a widely used index that is well-suited for the type of community data available to us, presence/absence data (Mason et al. 2013). Moreover, this index has been extensively associated with community assembly processes, ecosystem functioning, and delivery of ecosystem services (Petchey et al. 2004, Mason et al. 2013, Barbaro et al. 2017). I calculated γ FRic at the basin scale for both atlases. I used principal coordinate analysis (PCoA) to reduce the dimensionality of our trait data as FRic calculations become extremely difficult beyond several dimensions (Mouillot et al. 2021). I used the first 12 PCoA axes for γ FRic calculations because, beyond 12 axes, the calculation of FRic was computationally impossible. I also quantified and reported area under the curve (AUC) along with the percentage of the trait variation explained for our dimensionality reductions as suggested by Mouillot et al. (2021). AUC is a metric used to measure the correspondence between the original and reduced functional space, and it is based on Somer's D statistic (a measure of overlap in a multidimensional space). It is, therefore, appropriate to indicate the quality of trait dimensionality reduction (Mouillot et al. 2021). I then calculated the minimum number of PCoA axes required to meet the $AUC > 0.70$ criterion and to surpass the AUC elbow inflexion point, which is simply the number of PCoA axes beyond which the benefit (i.e., gain in AUC) increases more slowly than the cost (i.e., number of PCoA axes). I found that five and eight PCoA axes were required to surpass the AUC elbow inflexion point and the 0.70 threshold, respectively. See section 1.4.2 for more information regarding the quality assessment of the dimensionality reduction.

I calculated the functional counterpart of compositional β diversity as Sørensen-derived pairwise functional dissimilarity ($F_{\beta_{SOR}}$), which is composed of functional turnover ($F_{\beta_{SIM}}$) and functional nestedness ($F_{\beta_{SNE}}$). More information about the functional β diversity calculations is given in Appendix A.4. Due to the computational difficulty of calculating pairwise functional β diversity (Villéger et al. 2011, Mouillot et al. 2021), the maximum number of PCoA axes I could use for the

calculations was four. Since FRic calculation requires species richness to be higher than the number of traits (or PCoA axes) used (Laliberté et al. 2014a), I had to remove the communities with less than five breeding species from the analyses. There were a few grid cells with zero, and many grid cells with only a few breeding species in 2018, so I chose to use the first four PCoA axes as a compromise between the quality of the dimensionality reduction and the number of grid cells that I could include in our analyses. Consequently, I had to exclude one of the 34 communities in 1998 and 12 of the 34 communities in 2018 from our analyses.

I also calculated functional originality (FOri; Pavoine et al., 2005) for each species in the communities. The originality score of a species is the weight that maximizes the expected functional dissimilarity between two species randomly drawn from the species pool. In this case, maximum values are obtained when the functionally most distinct species have the highest originality values. I then compared the ranks of the extinct and extant species in each community in terms of their FOri to see whether the extinct species tend to be functionally more distinct. I used the first 12 PCoA axes (see above) to calculate FOri.

1.2.6 Dimensionality reduction

I followed Mouillot et al. (2021) to assess the quality of the dimensionality reductions I used prior to the functional richness (FRic) calculations. Due to computational limitations and the fact that I had to have species richness > number of traits (or PCoA) axes used in the FRic calculations (Villéger et al. 2008a), I had to exclude some of the 50 km x50 km grid squares from the analyses (for details, please see the manuscript). As a result, I ended up with two datasets, one of which was used at γ scale, where I used 12 PCoA axes, and at α and β scales, where I used 4 PCoA axes to calculate FRic. One of these datasets had some of the species missing (due to removal of the squares containing it), so the functional distances between the species pairs were slightly different in these datasets, which meant that I had to have two separate simulations to see how many PCoA axes were actually needed to

surpass the area under the curve (AUC) > 0.70 threshold and the AUC elbow inflexion point thresholds mentioned in Mouillot et al. (2021). I produced line graphs for the first 20 PCoA axes for each of the two cases to see how including additional PCoA axes changes the AUC value for the dimensionality reduction (Figure 1.2 and 1.3). The difference between the plots was negligible, yet I present them separately here. I found that the 12 PCoA axes easily surpasses both of the AUC thresholds (Figure 1.2), but when I used the first 4 PCoA axes, I could not surpass the AUC > 0.70 threshold and fell one PCoA axis short of surpassing the AUC elbow inflexion point.

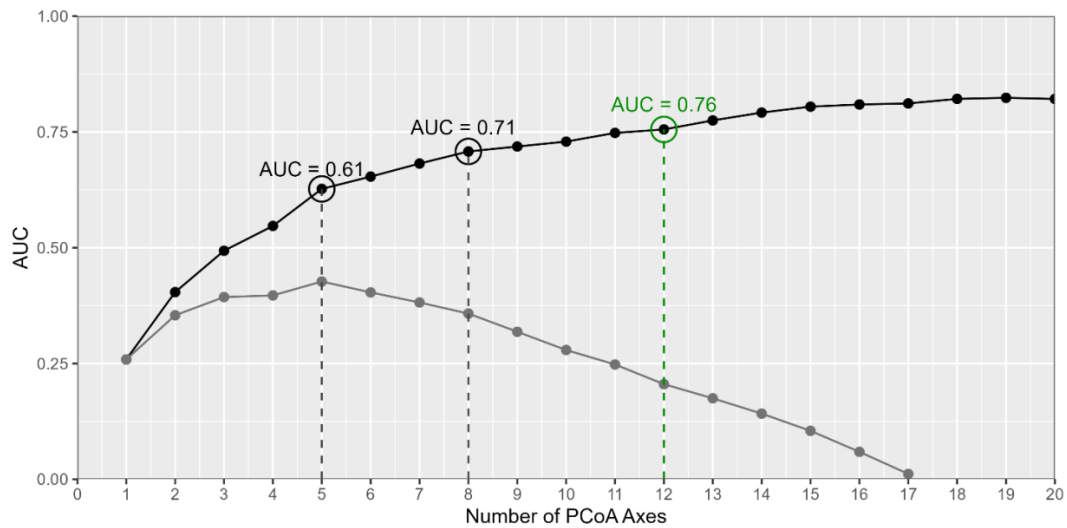


Figure 1.2 Relationship between AUC values for the dimensionality reductions and the number of PCoA axes used (black line with dots, where dots represent the data points), and the relationship between net AUC benefit (i.e., the gain in AUC minus the number of PCoA axes used (grey line with dots, where dots represent the data points) for the complete dataset. Black circles show the points where the elbow inflexion point (on the left - at 5 PCoA axes level) and the AUC > 0.70 (on the right – at 8 PCoA axes level) have been surpassed. The green circle shows where our dimensionality reduction's AUC value lies.

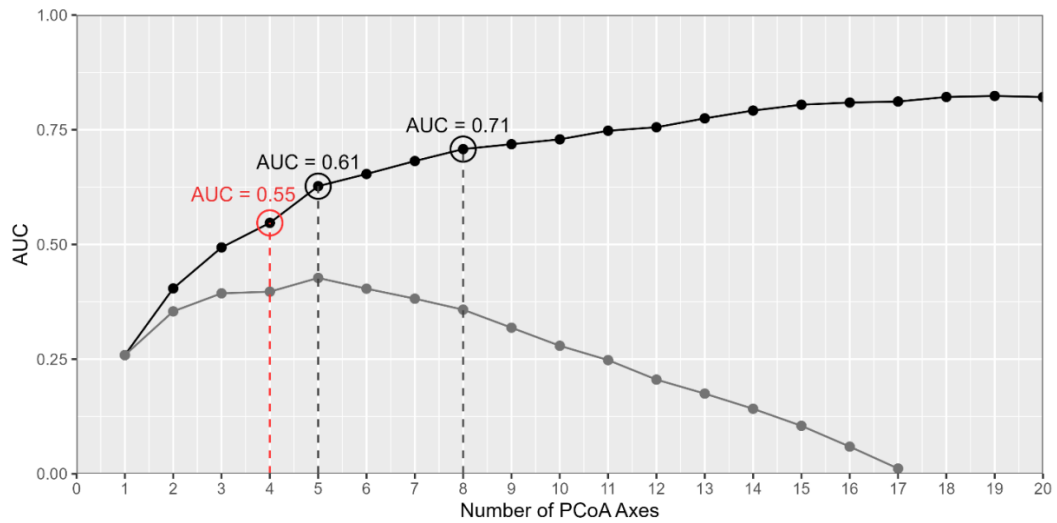


Figure 1.3 Relationship between AUC values for the dimensionality reductions and the number of PCoA axes used (black line with dots, where dots represent the data points), and the relationship between net AUC benefit (i.e., the gain in AUC minus the number of PCoA axes used (grey line with dots, where dots represent the data points) for the incomplete dataset, which didn't have some of the species. Black circles show the points where the elbow inflexion point (on the left - at 5 PCoA axes level) and the AUC > 0.70 (on the right – at 8 PCoA axes level) have been surpassed. The red circle shows where our dimensionality reduction's AUC value lies.

1.2.7 Calculation of diversity metrics and statistical analyses

I used R software (R Core Team 2024) for all biodiversity-related calculations and statistical analyses. I used *beta.pair*, *beta.multi* and *functional.betapart.core.pairwise* functions from the *betapart* R package (Baselga and Orme 2012) for the pairwise and multisite taxonomic and functional β diversity calculations. I utilized the *ecopart.multi* function from the *ecopart* R package (Tatsumi et al. 2022) to quantify the gain and loss components of the temporal change in multisite β diversity. I used the *dbFD* function from the *FD* package

(Laliberté et al. 2014a) to calculate FRic and *originality* function from the *BAT* package to calculate FOr (Cardoso et al. 2015). Lastly, I used the utilities of the *coRanking* R package (Kraemer et al. 2018) to calculate the AUC values for the dimensionality reductions. See section 1.4.2 for more information about the dimensionality reduction I conducted.

I built generalized linear mixed-effect models (GLMM; Zuur et al., 2009) to compare the species richness and FRic of the grid cells in 1998 and 2018, using year as the only predictor and grid cell identity (a factor with 34 levels) as the random effect in the models. I used the *glmmTMB* function from the *glmmTMB* package (Brooks et al. 2017) to fit the models. Model fit was assessed by visually examining the plot of residuals versus fitted values. I assessed the significance of the effect of the predictors (i.e., year) by checking whether 95% confidence intervals for the estimated effect sizes overlapped zero (Zuur & Ieno, 2016). I used the Wilcoxon test (test statistic= W , $\alpha = 0.05$ for all tests) to assess the significance of changes in the turnover and nestedness components of the taxonomic and functional β diversity between time periods.

1.2.7.1 Model structure

I used generalized linear mixed-effect models (GLMM; A. Zuur et al., 2009) to compare species richness, FRic at the α scale; that is, for the communities of the 50 km x 50 km study units. For species richness, which is a positive discrete numeric measure, I used a GLMM with negative binomial error distribution and log link functions to ensure positive fitted values. In this model, species richness was defined as the response variable and the year, which was a two-level factor (1998 and 2018), was defined as the sole explanatory variable, square ID and surface area of the squares (upon observing patterns in the species richness vs. area plots at the data exploration step) were defined as a random effects (34 and 31 levels, respectively) to be able to compare each square its own past or future-self and to allow for varying intercepts for the squares and area. For α FRic, which is a continuous numeric and

normally distributed variable (Shapiro-Wilk test; $p = 0.13$), I used a GLMM with Gamma error distribution and log link function. In this model, FRic was the response, the year was the only explanatory variable, and square ID (22 levels) was once again defined as the random variable, allowing for varying intercepts. Please see the R scripts published in association with the publication for the details of each model I built.

1.2.7.2 Model validation

GLMMs were validated by using the methods listed below:

(i) I plotted fitted values against residuals to check for heterogeneity (Zuur & Ieno, 2016). None of the models had any heterogeneity problem.

(ii) I plotted the residuals from the models against the predictors to see if there were any patterns in the plots. Some of the patterns could be solved by transforming the explanatory variables (such as log-transforming body mass in the brain mass ~ body mass model, see S3). None of the models had any problem at this point.

(iii) I used the utilities of the *DHARMa* package (Hartig 2018a) to check if the model predictions comply with the data, by using the *simulateResiduals*, *testDispersion*, *testOutliers* and *testZeroInflation* functions. To do that, I simulated 10,000 datasets for each model and run the test functions which test for over/underdispersion, zero-inflation, and outliers (Hartig 2018a). The models had no problem.

(iv) I checked for autocorrelation and partial autocorrelation in the model residuals by using *acf* and *pacf* functions from the *stats* package in R (R Core Team 2021). The spatial autocorrelation was checked by using the *testSpatialAutocorrelation* function from the *DHARMa* package. No patterns were observed in *acf* and *pacf* plots, and the models had no significant spatial autocorrelation in their residuals.

(v) I checked whether the null models performed better than our models by checking their AIC values. The models performed significantly better ($\Delta AIC > 2$) than the null models.

Please see the R scripts given in Appendix A.6 for the details of the model validation processes for the models.

1.3 Results

1.3.1 Taxonomic diversity

Breeding wetland bird species richness in KCB declined from 120 to 97 between 1998 and 2018 at the γ scale, representing a decline of around 19%. Twenty-seven breeding wetland bird species went extinct in the region, while four species colonized the basin. At the α scale, I observed net declines in the number of breeding wetland bird species for all grid cells, with a mean decline of ~19 species per grid cell (Figure 1.4). The decline in species richness was significant, with 2018's communities having lower overall species richness ($p < 0.001^{***}$).

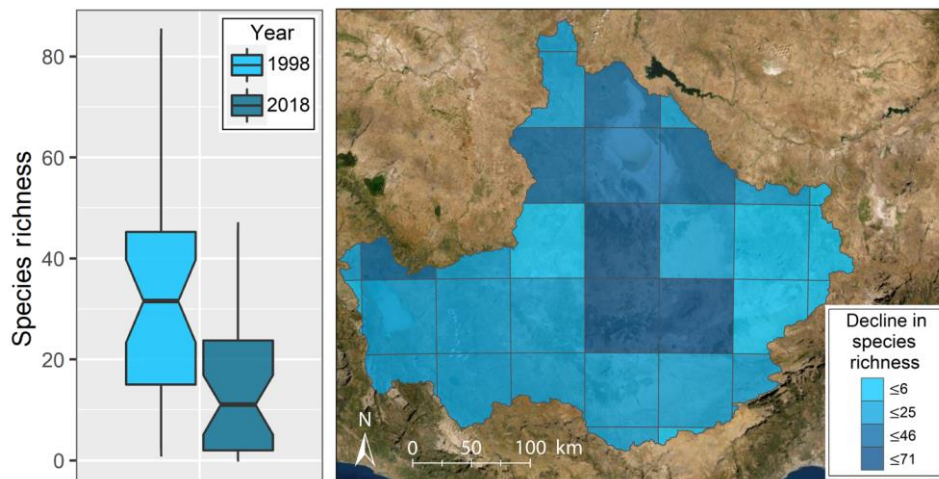


Figure 1.4 Box plot (a) and map (b) showing the change in breeding wetland bird species richness in Konya Closed Basin between 1998 and 2018 for the 50 km x 50 km grid cells.

At the β scale, I found that pairwise β_{SIM} and β_{SOR} were higher (Figure 1.5a; Wilcoxon test; $W = 49,890$, $p < 0.001^{***}$ and $W = 51,614$, $p < 0.001^{***}$, respectively) and β_{SNE} was lower ($W = 128,234$, $p < 0.001^{***}$) in 2018, as compared to 1998. I also found that, between 1998 and 2018, multisite β_{SOR} and β_{SIM} increased from 0.91 to 0.94 and 0.74 to 0.82, respectively, while β_{SNE} decreased from 0.17 to 0.12. Our partitioning of extinction and colonization components of temporal multisite taxonomic beta diversity showed that around 82% of the taxonomic differentiation/heterogenization was explained by species extinctions. The biggest individual species contributions to the heterogenization came from the extinctions of previously (i.e., in 1998) common species.

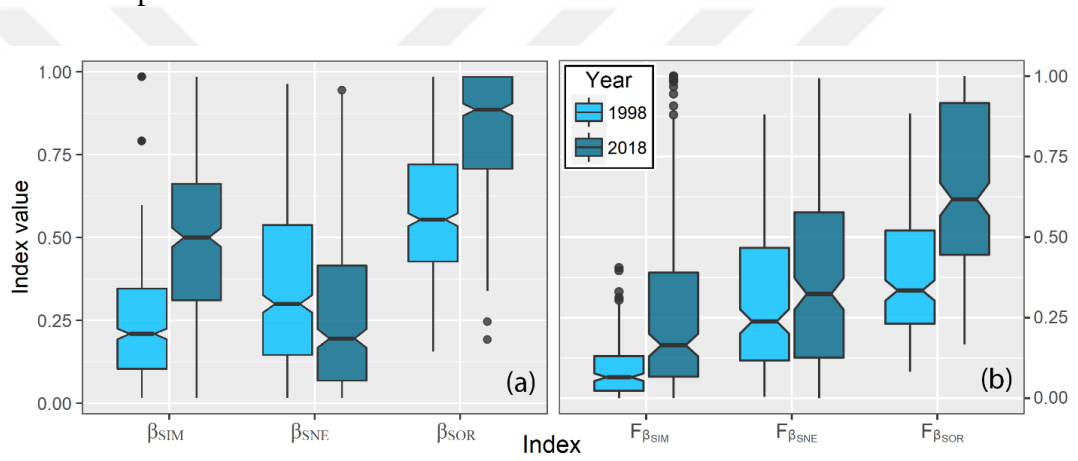


Figure 1.5 Compositional taxonomic (a) and functional (b) pairwise β diversity of the breeding wetland bird communities of the 50 km x 50 km grid cells in 1998 and 2018. β_{SIM} : taxonomic turnover, β_{SNE} : taxonomic nestedness-resultant dissimilarity, β_{SOR} : total taxonomic β diversity measured, $F_{\beta_{SIM}}$: functional turnover, $F_{\beta_{SNE}}$: functional nestedness-resultant dissimilarity, $F_{\beta_{SOR}}$: total functional β diversity measured.

1.3.2 Functional diversity

The number of PCoA axes used for the γ FRic and FOr_i calculations was 12, which exceeded both of the suggested AUC thresholds levels (Mouillot et al. 2021). This

dimensionality reduction resulted in a 50% explained trait variation and an AUC value of 0.75, which is considered a sufficiently good level of representation in functional diversity calculations (Mouillot et al. 2021). Because of computational limitations, the highest number of PCoA axes I was able to use in our β functional diversity calculations was four. This dimensionality reduction yielded an AUC value of 0.54 and failed to surpass both AUC thresholds suggested by Mouillot et al., (2021). Percent trait variation explained by the first four PCoA axes was 31%. Although this dimensionality reduction was suboptimal according to the AUC criteria of Mouillot et al. (2021), I still opted to use dimensionality reduction rather than manually and artificially eliminating some of the traits because of the potential and detrimental impacts of trait omission on functional diversity analyses (Zhu et al. 2017, Mouillot et al. 2021). Furthermore, the functional effects of some traits might arise from trait combinations, the number of which depends on the number of traits included in the study (de Bello et al. 2021b). I also considered that 31% of the variation in 74 traits/trait levels, which is far above the average number of traits used in other avian studies (Tobias et al. 2022), is still a substantial amount of information, justifying keeping this approach in our analysis. However, I invite our readers to keep this limitation in mind while interpreting our results.

I found that γ FRic declined by 66% between 1998 and 2018, which is 3.4 times higher than the decline in γ taxonomic richness. The communities of 2018 had significantly higher pairwise $F_{\beta_{SIM}}$ (Figure 1.5b; Wilcoxon test; $W = 12,444$, $p < 0.001^{***}$), $F_{\beta_{SOR}}$ ($W = 9,722$, $p < 0.001^{***}$), and $F_{\beta_{SNE}}$ ($W = 19,317$, $p = 0.03^*$). I also found that the total volume loss in the shared parts of the functional space occupied by the community pairs was, on average, 2.2 times greater than in the non-shared parts, and α FRic of the communities of 2018 was significantly lower than those of the 1998 communities ($p = 0.03^*$).

I discovered that, in 82% of the communities suffering from species richness declines between 1998 and 2018, functionally most distinct species (i.e., the species with the

highest FOr_i value) became extinct. I also found that, on average, the extinct species tended to rank 15% higher in terms of FOr_i, compared to the extant species.

1.3.3 Changes in lake surface areas

Remote sensing analyses showed substantial declines in lake surface areas between 1998 and 2018, varying according to the time of the season: the decline in surface area was, on average, 29% in the early breeding season and 88% in the late breeding season (Figure 1.6).

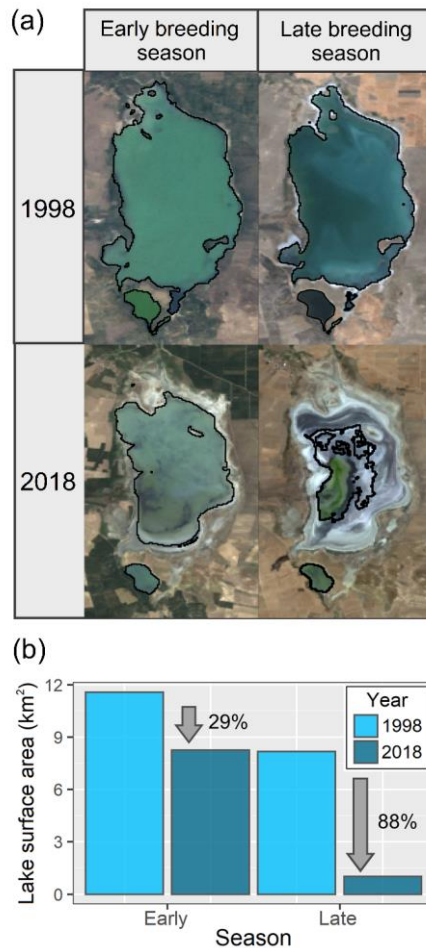


Figure 1.6 (a) Satellite images showing an important bird area (IBA) from Lake Kulu (Appendix A.1) at different stages of the breeding season in 1998 and 2018 and (b) average change in surface areas of the seven lake IBAs in the basin in 1996, 97, and

98 (shown as 1998 in the figure) and 2016, 17, and 18 (shown as 2018 in the figure) in the early and late breeding season.

1.4 Discussion

I used two breeding bird atlases and satellite imagery to investigate taxonomic and functional diversity of breeding waterbirds and how the phenology of shrinking/drying of lakes changed following a two-decade period of widespread wetland degradation, uncontrolled water extraction, and climate change at different spatial scales. To our knowledge, our study is the first to utilize trait-based approaches to investigate the multiscale outcomes of wetland degradation on wetland birds. Below, I discuss the mechanisms that can result in the observed changes in taxonomic and functional diversity along with their ecological consequences and conservation implications, and show how uncontrolled water extraction and increasing summer temperatures and the resulting advances in the timing of seasonal wetland shrinking might be contributing to the decline of some late-breeding wetland birds.

1.4.1 Compatibility of the datasets and selected breeding codes

1998's breeding bird atlas was conducted in our study area, Konya Closed Basin, and it was conducted in the breeding season of 1998, between 9 May 1998 and 30 June 1998 (Eken and Magnin 2000). The basin was divided into 10 km x10 km UTM grid squares. The teams used point counts and line transects (Bibby et al. 2000) (while moving between the point count spots) to survey the breeding birds in the basin. The atlas used the breeding codes given in Hagemeijer & Blair (1997). Two to six point transects were conducted in each 10 km x10 km square, and the points were chosen as to represent the full range of available habitats in each square. These spots were picked by using a detailed habitat map of the squares. Expert

ornithologists carried out the surveys. The results of the atlas were reported at both 10 km x 10 km and 50 km x 50 km scales.

2018's atlas was conducted at the national scale (Boyla et al. 2019), but as a part of the European Breeding Bird Atlas 2 (EBBA2; Keller et al. 2020). The breeding season for the study area was defined as the time frame between beginning of April and end of June, and it was divided into two periods: early breeding season and late breeding season. Among the early breeding season surveys that were conducted in our study and uploaded on eBird, ~69% were conducted in May, increasing the temporal compatibility of the two atlases used in the current study. In each of the 50 km x 50 km UTM grid squares, at least two 10 km x 10 km squares were surveyed by teams made up of a mixture of experts and volunteers. These 10 km x 10 km squares were chosen so that they are different in terms of their habitat types, and represent the 50 x 50 km habitat types well. The teams walked two to four 1 km transects (not necessarily straight lines) in an hour in each 10 km x 10 km square and recorded every species they saw or heard. The teams also stopped at random points for short durations along the transects to do some extra point-transect-like observations. The same breeding codes in Hagemeyer & Blair (1997) were used. In addition to the line transects, the teams also gathered data while they were on the move between line transects. The teams also conducted supplementary surveys, effort allocated to which substantially exceeded the total effort allocated to the systematic surveys, in each 50 x 50 km if they believe they were missing some different types of habitats or species. The atlas also utilized expert opinion, which used the distribution modelling output from the EBBA2 (Keller et al. 2020) and reviewed/curated citizen science data coming from eBird and a national birdwatching databases, which has been integrated into eBird (Cornell Lab of Ornithology 2025). The results of the atlas were reported only at 50 km x 50 km scale.

When using breeding bird atlases conducted at different time periods, with different methods, with different efforts, and by different teams, there is always the possibility of lack of comparability and compatibility, which may jeopardize the subsequent

analyses (van der Hoek et al. 2015). I think that the two atlases used in the current study were comparable and compatible enough in terms of the output they generated (i.e., the incidence data) for several reasons. First, the grid system used in the atlases perfectly overlap: the same exact grids and squares were used in both of the atlases. Second, the breeding codes used were the same with addition of a single code for suspected non-breeders in the more recent atlas (Herrando et al. 2013). Third, the methods used in the atlases were similar: 1998's atlas used a combination of line and point transects and 2018's atlas used line transects with some stationary recording at random intervals. I expect these two similar approaches to produce comparable presence/absence data (Sutherland et al. 2004, Buckland 2006, Sutherland 2006). Besides, the 2018's atlas had extensive and opportunistic supplementary surveys that allowed the observers to collect data from not only the 10 km x10 km squares that they systematically surveyed, but also from other 10 km x10 km squares from the same 50 km x 50 km square, which can partly compensate for the shortage of systematic effort in 2018 (when compared to the 1998's atlas). However, I still thought that the differences in the effort spent on the standardized part of the surveys of the atlases (i.e., point and line transects) may jeopardize comparability, although the atlas with less effort, which is the 2018 atlas, had expert opinion and supplementary surveys that helped it achieve a more complete species checklist for the squares, and match the 1998's atlas in effort. To test whether the species extinctions and colonizations deduced from the differences between the two atlases were accurate, I used expert opinion and some local studies. I chose 12 species (10 waterbirds – 2 reed warblers – nearly 10% of the study species) from the list of the study species (Appendix A.2) and plotted their 1998 and 2018 distributions on a map, along with eBird sightings between 2014-2018. The authors were able to confirm all extinctions for 9 out of the 10 waterbird species, but had to consult an experienced researcher from Turkish Bird Record Committee, Kuzey Cem Kulaçoğlu, to confirm extinctions in two 50 km x 50 km squares for the tenth species. I found all of the extinctions deduced from the atlas studies were accurate. Confirming some of the extinctions was relatively easy (e.g., confirmation of extinction of waterbirds in

squares where the wetlands totally disappeared), but for some other species, the authors had to use their own survey data (e.g., Özgencil, 2016, 2019; Özgencil et al., 2021) to confirm the extinctions. For the two reed-dwelling passerines, once again, the authors have used their own field data from 2018 and 2019 (Özgencil 2019) and curated eBird records from 2013-2018 (Cornell Lab of Ornithology 2025), which reported presences of all birds detected (i.e., complete checklists). Since the data was available for 17 out of the 22 instances that the two chosen passerines, Eurasian Reed Warbler (*Acrocephalus scirpaceus*) and Great Reed Warbler (*Acrocephalus arundinaceus*), had gone extinct according to the datasets, I could only conduct our test on these instances. I found that the extinctions conformed to the extinctions deduced from our datasets in 15 of the 17 cases (~88%). For the remaining two, although the 2018's atlas data suggested that the species were extinct, they actually were not as they were detected in some of the observations conducted as a part of the corresponding my fieldwork in 2018 and 2019. The reason why they were not present in the 2018's atlas results is probably because the findings of the fieldwork were not submitted as checklists on eBird. If they had been submitted, they would have appeared in the final output of the 2018's atlas.

Breeding bird atlases generate data that is essential to document changes in distribution and diversity of birds (Pototsky and Cresswell 2023). Such data comes in handy in especially in understudied areas like our study area (Donald and Fuller 1998). There have been hundreds of studies that used breeding bird atlases for various purposes such as assessing population status of birds (e.g., Burfield et al. 2023), training species distribution models (e.g., Soultan et al. 2022), and detecting range shifts (e.g., Howard et al. 2023). Many of these studies utilized atlases conducted at different times, by different teams using different methods. Among these studies were studies that compared the first European Breeding Bird Atlas (EBBA1; Hagemeijer and Blair 1997) and the second European Breeding Bird Atlas (EBBA2; Keller et al. 2020), which have notable differences within and between in terms of the field methods and effort spent (e.g., Soultan et al. 2022; Howard et al. 2023). Some studies even used atlases from widely separated regions that were

conducted by different teams using different methods, at different times to study taxonomic and functional features of breeding bird communities (e.g., von Euler and Svensson 2001). All of these studies employed the shared ability of atlases to generate large and detailed maps of distribution data despite some variation in field methods (Beck et al. 2018). Accuracy of representation in atlas can be further enhanced by including citizen science data. Despite their shortcomings, utilizing citizen science remains the most practical way to achieve huge quantities of presence/absence data over large areas (Devictor et al. 2010, Keller 2017, Butler et al. 2021, Pototsky and Cresswell 2023). Because of their longer and higher seasonal coverage, citizen science data on platforms like eBird can actually achieve highly complete representations of local community composition and capture high number of species (Butler et al. 2021). Expert opinion is another source of data capable of complementing atlas studies, and they proved to be especially useful in understudied areas, where they can help researchers generate accurate distributional data (e.g., Kalyakin et al. 2022). The second breeding bird atlas used in this study, the 2018 atlas, utilized both citizen science data and expert opinion (coming from different sources, including eBird; Boyla et al. 2019). Together with the supplementary surveys (the non-standardized surveys mentioned in the preceding paragraph), these must have helped the second atlas achieve a comparable output to that of the first atlas. However, I acknowledge that comparing successive atlases that differ in their survey methods poses a challenge. After all, whether a species is detected or not during a survey will surely depend on the amount of effort spent (Greenwood 2017, Herrando et al. 2019). However, even in regions with relatively high numbers of experts and fieldworkers, there will always be some difference in coverage and effort across different localities in atlas work (Keller 2017). Besides, no atlas guarantees to fully and totally capture all of the bird species in an area. Instead, the atlases studies rather acknowledge the fact that some rare or even common species can be missed even in areas that have been relatively well-surveyed. For instance, despite the participation of thousands of fieldworkers and a four-year data collection period, it is estimated that the observers were able to see or hear less than 5% of all bird

individuals in Scotland during their breeding bird atlas study (Gibbons et al. 1993, Donald and Fuller 1998). Additionally, one may also argue that the different field methods employed; that is, line transects and point transects in 1998 and line transects with pauses in 2018, can generate incomparable bird presence-absence data. To see whether this is the case, I reviewed studies that compared the output of line and point transect surveys. I found that, the line and points transect methods tend to generate highly similar species compositions (compositional overlap: 85-91%) and richness values (richness difference: 0-15%) across different types habitats of habitats, including forests, marshland, open areas, grassland, and arid shrublands (Fletcher et al. 2000, Cai et al. 2010, Nalwanga et al. 2012, Taulman 2013, Fontana et al. 2018, Pascoe et al. 2019). For the reasons listed above, I concluded that the distribution data generated in the two atlases used in this study were comparable and compatible enough to carry out the analyses that I employed here. However, I do acknowledge that the atlas studies have inherent weaknesses (like any other survey method), yet with the help of complementary data sources, such as citizen science data and expert opinion, the accuracy of atlases can further be enhanced like in the case of the second breeding atlas used in this study. Given these and the fact that ground-truthing using detailed and reliable data also validated nearly all of the extinctions/colonizations (total success rate for the 12 sample species: 97%) of a sample of study species deduced from comparison of the two atlas studies (see the preceding paragraph), I conclude that the two atlas studies used have comparable output and the ecological conclusions drawn from the large-scale changes in diversity and distributions constitute a reliable representation of the true changes that have taken place from 1998 to 2018.

However, the two atlases do differ in their methods and discovering how this potential weakness in our data can affect the results is crucial. First, if the second atlas is indeed consistently lower in effort, despite the complementary surveys and data sources used (see above), this would present itself as lower species richness values in the second atlas, which actually is the case. However, some study squares in the region were indeed very-well surveyed and had hundreds of complete and

curated observations on eBird (which were employed in the second atlas), but they still had lower species compared to the first atlas, which further suggests the lower species richness values detected in this study may actually represent the reality. Second, if the lower effort in the second atlas systematically caused failure to detect species occupying certain parts of trait space or functional space, then this would certainly result in biased trait-based analyses. Guessing the influence this would have on the results of the analyses is difficult because direction and nature of the bias would depend on the functional trait values of the species missed. I plotted the 15 species with the highest numbers of deduced extinctions in functional space to have an idea about whether the deduced extinctions, some of which can be false-absences resulting from lower effort in the second atlas, are concentrated in certain parts of the functional space (Figure 1.7). A visual inspection of these species' positions in the functional space suggested no such problems, although species with certain traits are indeed expected to have gone extinct more often, such as those that forage in water and nest in wetlands. These species apparently went extinct more often than the others despite the presence of functionally very similar species nearby.

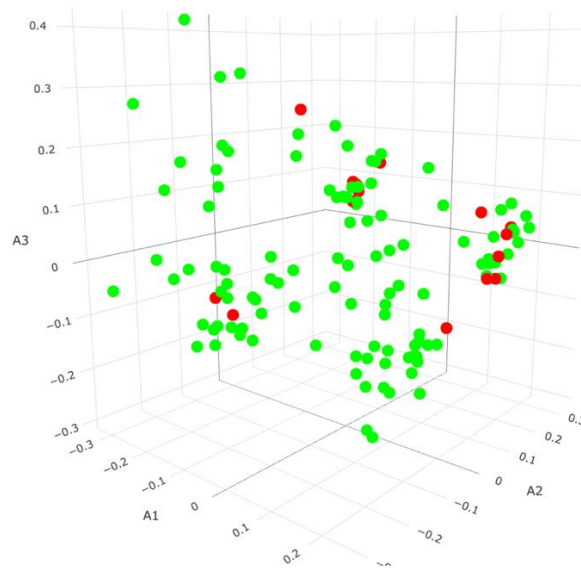


Figure 1.7 The 15 bird species with the highest number of extinctions (red dots) plotted in functional space (the first three PCoA axes – see the main text for more on this) alongside the other species (green dots).

Consistent failure to detect species occupying certain parts of the functional space would potentially have other signatures in the data. For instance, if lower effort was indeed a problem, I would expect a lower proportion of smaller species detected in the second atlas. This is because larger species tend to be more easily detected (Reynolds et al. 1980, Johnson 2008). However, this was opposite of what I found: there was a decline of 26% in community-weighted mean of body mass trait across the study squares, which is also in line with findings of previous studies (Gaston and Blackburn 1995, Cardillo 2003, Gardner et al. 2011, Whytock et al. 2016, Ripple et al. 2017, Chichorro et al. 2019). Furthermore, if the detection failures did indeed happen, either randomly or systematically within the functional space, I would expect to find changes in community-weighted means that would not make ecological sense or do not conform to findings of other studies. This was, once again, opposite of what I found. For instance, I discovered a 25% decline in foraging by diving and 11% decline in reed-nesting traits across the study squares. Both of these changes are expected to happen when the wetlands are disappearing like they did in

our study area (Yılmaz et al. 2021). I also found a 42% increase in community-weighted mean of the relative brain mass trait (or residual brain mass), which is also expected and observed in other parts of the world (e.g., Sayol et al. 2020). Nevertheless, I acknowledge the lack of perfect incompatibility in the data sources used in this study and the readers should view the results and conclusions given here in the light of this potential weakness.

I used all types of breeding records, which are possible, probable, and confirmed-coded records (Hagemeijer and Blair 1997) to be more inclusive because I realized that for some of the species, such as reed-nesting passerines (Passeriformes), the confirmed-coded records were lacking, possibly resulting in a bias in the dataset. I think most of the possible-coded breeding species are indeed breeding in the basin, and it seems like these species' breeding codes stayed low only because of the difficulty of obtaining high breeding codes within some challenging habitats and because of shy nature of some of the species. For the 1998's atlas, I had no means of checking the validity of this assumption, but to check it for the 2018's atlas, I chose a couple of relatively well-known and common species to see whether they truly are breeding in places where non-confirmed records were given. For this purpose, I chose Eurasian Reed Warbler (*Acrocephalus scirpaceus*) and Great Reed Warbler (*Acrocephalus arundinaceus*), and used field data collected by myself during one of my past studies (Özgencil 2016, 2019) aiming at surveying wetlands in the region for other wetland bird species. These past surveys did not focus on these species, but they reported the presence of all the species that were identified. I saw that in some grid squares where I had the past survey data of the two species and non-confirmed breeding records in 2018's atlas, the two species were present throughout the summer. I consider this is as a good sign that the species were actually breeding there. I also think that the same is probably true for most of our study species with non-confirmed (i.e., possible and probable-coded) breeding records. Of course, there is no means to test it for every study species and every grid square. I just opted to be more inclusive by choosing to use the possible-coded records as well because, after all, I used them for both atlases (keeping comparability) and the species with the

“possible” codes that were actually not breeding in the related squares probably constitute only a tiny fraction in the dataset. Besides, literature is full of studies that treated breeding evidences from all levels of certainty, including the possible level, as a sign of presence (e.g., Ma & Zhang, 2015; Polakowska et al., 2012; Šímová et al., 2015). Conversely, there are some other studies that opted to use only the probable and confirmed-coded records (e.g., Titeux et al., 2004; Venier et al., 2004). I acknowledge that this decision poses a trade-off. On the one hand, being more inclusive may possibly generate a more complete breeding bird community, higher sample size, but some non-breeding species may be wrongly labelled as “breeding”. On the other hand, being more conservative and sticking with only the higher levels of breeding evidence may allow one to more reliably estimate true breeding status, but this comes with the cost of lower sample size and exclusion of some breeding species that ended up with possible breeding codes only because of their cryptic nature or low population size. Here, I chose to be more inclusive by including the possible-coded records, and our results should be viewed by keeping in mind the pros and cons of such an approach.

When I was dealing with the marginal grid squares, I only used the records that fell within the basin boundaries. This was easy to do for the 1998’s atlas because the results were also available at 10 km x 10 km resolution. For the 2018’s atlas, the final results were available only at 50 km x 50 km resolution, but luckily, all of the observation records were submitted to the eBird database (Cornell Lab of Ornithology 2025). I downloaded these records and overlaid them on a map in ArcGIS Pro 2.3 (ESRI, 2018), and included the records that were from within the basin’s boundaries.

In this study, I focused on wetland bird species, here defined as the species that had “freshwater” listed in their system and/or any type of “inland wetland” habitat in their habitat type in IUCN’s database (IUCN 2015). Wetland birds defined in this way will therefore include all waterbirds that depend on wetlands for their reproduction and survival (e.g., ducks, geese, and swans) as well as species that are not aquatic but depend on this ecosystem, such as the Common Cuckoo (*Cuculus*

canorus) and Common Reed Warbler (*Acrocephalus scirpaceus*). This procedure eliminated species that occur around wetlands but do not significantly depend on or directly inhabit wetland habitats such as the Eurasian Skylark (*Alauda arvensis*). The full list of species included, which included 124 species, can be found in Appendix A.2. Diversity of the breeding wetland bird communities

The widespread taxonomic diversity losses that I observed at the α scale left the grid cells taxonomically more heterogeneous between them, as indicated by the increased total taxonomic β diversity (β_{SOR}). Increases in the turnover-resultant dissimilarity (β_{SIM}) and decreases in the nestedness-resultant dissimilarity (β_{SNE}) point to a clear shift from nestedness dominance to turnover dominance in taxonomic β diversity (Fig. 3a). This suggests that, in 1998, most of the compositional differences between the local patches (i.e., the grid squares) were due to community nestedness, while in 2018, the differences were mostly due to communities having species that are not present in other communities (Baselga, 2010). When evaluated in conjunction with the widespread species losses at the local scale and the fact that 82% of the taxonomic heterogeneity observed resulted from species extinctions, these changes in taxonomic β diversity point to an undesirable (from a conservation perspective) phenomenon referred to as “subtractive heterogenization” (Kessler et al. 2009, Socolar et al. 2016). (Kessler et al. 2009, Socolar et al. 2016) Consequently, while preserving the remaining taxonomic diversity in 2018 would require large-scale conservation efforts to capture the more heterogeneously distributed diversity, most of the taxonomic diversity could have been preserved just by protecting a few highly diverse areas back in 1998 (e.g., the grid cells in the center in Fig. 2b) (Socolar et al., 2016). Therefore, preventing further degradation and loss of important wetlands across the entire basin, rather than focusing on a few specific wetlands, should be a conservation priority to preserve the remaining diversity of wetland birds.

The heterogenization I detected in our study area goes against the findings of some studies in other study systems which documented widespread homogenization across various taxa (Baiser et al. 2012, Finderup Nielsen et al. 2019, Leroy et al. 2023). In our case, heterogenization was caused by extinctions of widespread species, which

may be an early response to habitat degradation, leading to a temporary increase in beta diversity (Socolar et al. 2016). However, as wetland degradation and loss continue, beta diversity will more likely decline due to homogenizing effects of loss of rare species (subtractive homogenization) and domination of a few generalists (additive homogenization). The fact that widespread species disappeared first is alarming because it speaks for itself regarding the large-scale dimension and intensity of wetland degradation.

I also found that the decline in functional richness (FRic) at the scale of the basin was far greater than that of species richness, a pattern that has been reported in other studies (e.g., Hooper & Ashton, 2020; Tinoco et al., 2018). This finding demonstrates the importance of considering the multifaceted nature of biodiversity to gain a thorough understanding of the consequences of habitat degradation and loss for biodiversity (Si et al. 2016, de Bello et al. 2021b). Previous studies have suggested that the change in functional diversity will expectedly exceed the change in taxonomic diversity (*i*) in communities with high mean functional distinctness, because species losses and gains will mostly affect unique trait combinations, (*ii*) when the new colonizers or extinct species are the functionally distinct ones, and (*iii*) at smaller scales as biotic interactions, which can increase mean functional distinctness, are expected to be stronger at the local scale (Toussaint et al. 2021). In our case, the second point seems to have been the major driver because the extinct species were functionally more distinct (see below). The first and third points were of less importance because birds depending strongly on wetland habitats usually have strict habitat requirements, implying that the environmental filtering may still play an important role in the assembly of wetland bird communities and lower mean functional distinctness at the local scale (Özgencil et al. 2020).

The observed declines in γ FRic and α FRic in 2018 imply that some of the niches either disappeared or remain unoccupied, which can potentially hinder ecosystem functioning and reduce the communities' capability to buffer environmental changes (Mason et al. 2005a, Mouillot et al. 2013). The declines in functional diversity at regional and local scales (γ FRic and α FRic, respectively) suggest that functional

homogenization had taken place at local and regional scales over the study period (Ibarra and Martin 2015). Loss of functionally distinct species in bird communities, as it occurred in our study system, is a common outcome of habitat disturbance and degradation (e.g., Devictor et al., 2008; Liang et al., 2019). Such losses can have detrimental consequences for ecosystem functioning and the delivery of ecosystem services, as some of these functionally original species likely played irreplaceable roles in their ecosystems, as evidenced by the observed declines in the functional diversity (Clavel et al. 2011, Yılmaz et al. 2021). This functional homogenization happening at γ and α scales is different from the subtractive heterogenization at landscape or β scale, where the individual study communities (in the grid cells) became more dissimilar.

Our functional β diversity analyses showed that the nestedness dominance in functional β diversity persisted in 2018 (Fig. 3b). Thus, I found a contrasting behavior of the nestedness components of the taxonomic and functional β diversity: declining taxonomic nestedness and increasing functional nestedness (Fig 3). Such contrasting patterns have been documented in other studies as well (e.g., Si et al., 2016). The particular pattern that I observed may appear if the shared or widespread species that have gone extinct are the functionally distinct ones. In such a case, proportionately larger declines in the overlapping parts of the trait volume occupied by the communities would be expected. If most of the extant species in one community are functionally similar to species in other communities too (as expected from the decreased γFRic), then the result would be an increase in the nestedness between communities in trait space. However, the increased $F_{\beta\text{SIM}}$ implies that some of the communities still possess few functionally distinct species that are not found in the other communities. If additional functionally unique species are lost occur due to extinction debt (Kuussaari et al. 2009) or further habitat degradation, then the communities may be vulnerable to further dramatic declines in functional diversity and functional homogenization. Unfortunately, although the resultant communities are functionally more nested as demonstrated by the increased $F_{\beta\text{SNE}}$ it is no longer possible to protect the remaining functional diversity by conserving the functionally

richer communities alone due to the accompanying increase in $F_{\beta_{SIM}}$ (Fig. 3b). Therefore, conservation efforts should be focused on protecting wetlands across the whole basin to conserve the remaining unique avian ecological functions and trait combinations and to avoid further functional homogenization at local scale. A recent study showed that it may be difficult to bring back the original functions and combinations of waterbird traits once a wetland loses its natural state and that artificial reservoirs fail to reach the functional diversity levels of the natural wetlands (Almeida et al. 2020). Hence, protection of the remaining wetlands in their natural states and their restoration across the whole basin should be the main conservation target, keeping in mind that even the restored wetlands may not be able to provide the original functions and diversity.

1.4.2 Earlier shrinking and drying of the lakes

I found that the wetlands in the basin were shrinking and drying earlier in the breeding season in the late-2010s than in the late-1990s, as demonstrated elsewhere (e.g., Rashford et al., 2016). A recent study conducted in KCB showed that the increases in temperature and pan evaporation were significantly more intense in the summer (Ekercin et al. 2019). In addition, in the early-2000s, a widespread shift from non-irrigated agriculture to irrigated agriculture began, increasing the water demand and water extraction from wells in the summer, and the number of irrigation dams in the basin (Yilmaz et al. 2021). The combined effect of these pressures helps explain the fact that wetlands in the region are starting to dry up earlier.

Diving waterbirds may consume the same food sources as non-diving waterbirds (Kear 2005) and spatial segregation of foraging microhabitats can be an important way to partition food resources between the two groups (Amat 1984, Chatterjee et al. 2020). Therefore, earlier shrinking of the wetlands in KCB might potentially enhance the competition between the late-breeding, globally-threatened diving ducks and non-diving waterbirds by forcing a greater niche overlap between them. This hypothesis is illustrated in Figure 1.8. Lakes in our study area are relatively shallow

and have relatively flat morphometries (Eken et al. 2006). Therefore, unlike lakes with steeper morphometry, the surface area of these lakes is expected to be closely linked to water level. When lakes remain sufficiently large and deep during the breeding season, as was likely the case in 1998, (the upper row in Figure 1.8), diving ducks can access their exclusive deep foraging areas, thereby minimizing foraging microhabitat overlap with non-diving waterbirds. However, when lakes shrink and get shallower during the breeding season, as likely occurred in 2018, diving ducks may be forced to utilize the shallower parts of the wetlands, where they need to compete for food and other resources (e.g., roosting sites) with non-diving waterbirds (lower row in Figure 1.8). Such fluctuations in surface area and water level are intrinsic to wetlands in the study region (Beklioglu et al. 2001). However, advancing shrinking phenology may cause shrinking or drying events to occur in the middle of breeding season for the late-breeding diving ducks, potentially intensifying dietary competition with non-diving waterbirds. If wetlands dry up completely in late summer, the breeding of the late-breeding species may fail completely, as their young may perish before fledging.

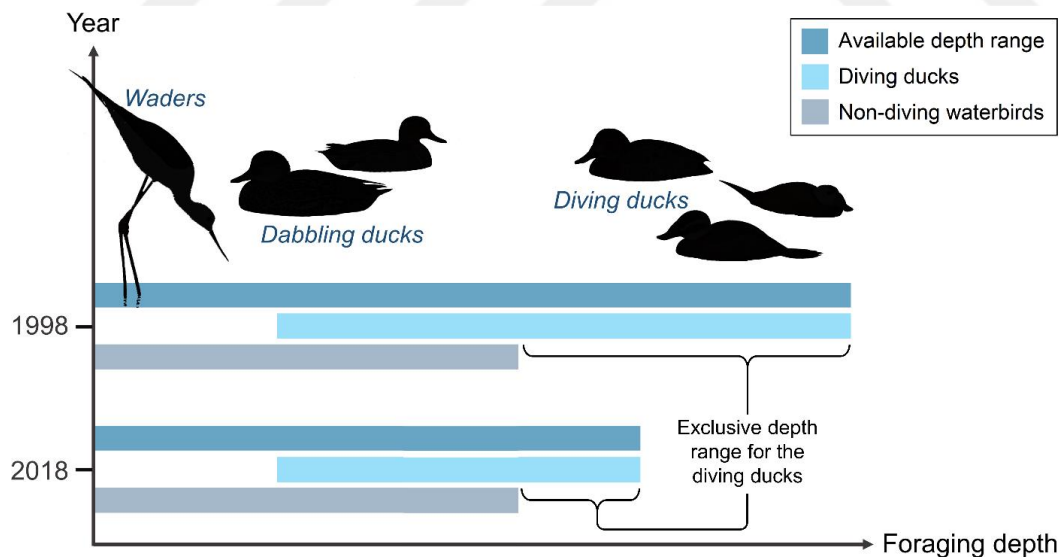


Figure 1.8 A hypothetical example demonstrating how earlier shrinking of wetlands and the resulting water level decline during the breeding season can escalate the competition between the endangered diving ducks and non-diving waterbirds.

To the extent of our knowledge, this study is the first to suggest that advancing in the timing of shrinking or drying of the wetlands due to climate change and increased water demand during the breeding season may be contributing to the decline of the already endangered late-breeding diving ducks such as Common Pochards (*Aythya ferina*) and White-headed Ducks (*Oxyura leucocephala*). This hypothesis remains to be tested with further observations. Nevertheless, urgent changes in agricultural policies are required to reduce the water extraction for irrigation, and better wetland management is required to minimize the late-season shrinking and maximize local wetland ecosystem services such as local climate regulation (Mitsch et al. 2015).

1.5 Author contributions

İbrahim Kaan Özgencil: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft. Mehmet Arda Çolak: Data curation, Formal analysis, Validation, Writing - original draft. Gültekin Yılmaz: Conceptualization, Data curation. Alaz Uslu: Data curation. Sarah Hasnain: Formal analysis. Meryem Beklioğlu: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing - review & editing. Christine Meynard: Conceptualization, Formal analysis, Investigation, Investigation, Methodology, Writing - review & editing. Zuhale Akyürek: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing - review & editing. Korhan Özkan: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Writing - review & editing. Erik Jeppesen: Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing - review & editing.



CHAPTER 2

FACTORS DRIVING TAXONOMIC AND FUNCTIONAL STABILITY OF BREEDING BIRD COMMUNITIES IN EUROPE

In this chapter, I used two breeding bird atlases conducted in Europe to study the effects of a wide range of extrinsic and intrinsic factors on temporal taxonomic and functional stability of breeding bird communities in Europe. I employed spatial error models (Bivand 2008) and identified a collection of variables that significantly alter temporal stability of breeding bird communities.

2.1 Introduction

2.1.1 Background

Biodiversity, the variety of life on Earth, is fundamental to the resilience and functionality of ecosystems and essential for human existence (Cardinale et al. 2012, Ceballos et al. 2015, Cowie et al. 2022). However, human activities, including habitat destruction, overexploitation, pollution, spread of invasive species, and climate change, have resulted in unprecedented loss of biodiversity. The current rate of species extinction is estimated to be 1,000 times higher than the background extinction rate (Pimm et al. 2014), with even higher rates predicted in the near future (McCallum 2015, van der Sluijs 2020). Many scientists believe that our planet is undergoing its sixth mass extinction, with extinction rates exceeding those of any previous mass extinction events (Barnosky et al. 2011, Ceballos et al. 2015, 2017; Cowie et al. 2022 - but also see Wiens and Saban 2025). At the conclusion of this mass extinction event, nearly 75% of its species are expected go extinct (Briggs 2017). Slowing the rate of biodiversity loss, which threatens both the delivery of critical ecosystem services and the stability of ecosystem processes, remains one of

the biggest challenges of our century (Barnosky et al. 2011, Dirzo et al. 2014). Although most of the focus has been on extinctions, studies suggest that other levels of biotic changes, such as declines in abundances, range contractions, and community reorganizations may have far greater impacts (Dirzo et al. 2014, Ceballos et al. 2017, Rosenberg et al. 2019). Previous research across various taxa has demonstrated that focusing solely on extinction rates may underestimate the magnitude and intensity of ongoing biotic changes (Ceballos et al. 2017, Rosenberg et al. 2019). Community reorganization, driven by species turnover and changes in species abundances, represents another form of biotic change, occurring continuously due to both natural and human-related causes (Olden and Rooney 2006, Godoy et al. 2024). This process arises because species are not equally vulnerable to decline in abundance in response to environmental changes, owing to differences in their intrinsic features such as their reproductive rates and dispersal capabilities (Devictor et al. 2008b). While the nature of the change is highly context-dependent, certain common patterns are widely observed, such as loss of specialist species with unique or rare functions in their ecosystems (Şekercioğlu et al. 2004). At higher levels of ecological organization, these changes have been found to frequently result in biotic homogenization, a process where ecological communities become compositionally, functionally, or phylogenetically more similar over time (Olden 2006, Olden and Rooney 2006). However, cases of biotic heterogenization, where communities become more dissimilar, are also widely documented (see Chapter 1; Socolar et al., 2016). Such community-level changes are expected have profound consequences for ecosystem functioning, resistance to further changes, and delivery of ecosystem services (Isbell 2010, de Mazancourt et al. 2013a). Therefore, studying and monitoring compositional changes in ecological communities is essential for predicting the outcomes of biotic changes.

Birds (class Aves, Linnaeus 1758) are the most-studied group of vertebrates that occur worldwide and found in nearly all habitat types (Whelan et al. 2008, Wenny et al. 2011, Tobias et al. 2022). There are slightly more than 11,500 species of birds in the world (del Hoyo 2019), and they provide many ecosystem services, with the

supporting and regulating ecosystem services, such as pest control and propagule dispersal, being the most significant ones (Şekercioğlu et al. 2004, 2016; Wenny et al. 2011). Previous studies have demonstrated that birds are highly capable pest controllers (Şekercioğlu et al. 2016, Barbaro et al. 2017) and disperse a variety of organisms, including plants, insects, and even fish (Hernández 2011, Şekercioğlu et al. 2016, Lovas-Kiss et al. 2020, 2024). Their impact on ecosystems is further amplified by their unparalleled movement capabilities, allowing them to deliver these services and get involved in ecological networks over vast areas (Whelan et al. 2008). Furthermore, birds can serve as excellent bioindicators of certain environmental factors trophic state and water quality of aquatic systems (Gregory et al. 2003, Özgencil et al. 2020, Fraixedas et al. 2020). Some birds also play irreplaceable or keystone roles in their ecosystems, such as woodpeckers, which create nesting cavities that are subsequently used by a wide range of other organisms (Stocker and Irvine 1983, Montague-Drake et al. 2011, Gaston 2022).

Despite their ecological importance, birds are as threatened as, if not more than, many other organism groups (Şekercioğlu et al. 2004). According to the most recent assessments by the International Union for Conservation of Nature (IUCN), 12% of the assessed birds face extinction (IUCN 2024). The IUCN reports that 169 bird species are now classified as extinct or extinct in the wild (IUCN 2024). Rosenberg et al. (2019) reported a mean decline of 29% in abundances of birds since the 1970s in North America, with the declines being not restricted to rare or endangered species. Similarly, Burns et al. (2021) documented a 17-19% decline in bird abundances within the European Union since the 1980s. Research have shown that some groups of birds are more prone to declines, including those inhabiting agricultural landscapes (e.g., Böhning-Gaese & Bauer, 1996; Donald et al., 2006; Rigal et al., 2023), scavengers (e.g., Buechley & Şekercioğlu, 2016), insectivores (e.g., Bowler et al. 2019), seabirds (e.g., Paleczny et al., 2015), and migratory species (e.g., Sanderson et al., 2002). Moreover, compositional and functional changes in bird communities have also been well-documented across various habitats in different parts of the world, such as widespread losses of functionally specialized

species (Drapeau et al. 2000, Devictor et al. 2008a, Lindström et al. 2013, Özgencil et al. 2020). These declines and changes underscore the urgent need to understand and address threats faced by bird populations, which could help prevent further losses and alleviate the associated impacts on ecosystem integrity, processes, and services (Şekercioğlu et al. 2004, Rosenberg et al. 2019, Gaston 2022).

Traditional taxonomic approaches to quantifying biological diversity treat all species equally different, disregarding their phylogenetic relatedness and the fact species perform different ecological functions (Villéger et al. 2011, Si et al. 2016, de Bello et al. 2021b). As an alternative or complement of taxonomic approaches, trait-based approaches focus on the properties of organisms, known as functional traits, rather than on the species themselves (Martini et al. 2021). Functional traits are defined as morphological, physiological, behavioral, or phenological properties of organisms that influence their growth rate, reproductive output, and/or survival of organisms or their contribution to ecosystem functioning and are measurable at the individual level, without any reference to the environment or any other level of ecological organization (Violle et al. 2007b, Luck et al. 2012, de Bello et al. 2021b). By their definition, functional traits are expected to determine how species respond to disturbances or changes in ecosystems, how they interact with one another, how well they will perform under specific conditions, ultimately shaping species tolerances, distributional limits, ecosystem functions, and patterns of coexistence (Lavorel et al. 2011, Cadotte et al. 2011, Carmona et al. 2016). Consequently, focusing on functional traits, rather than species identities, allows trait-based or functional approaches to better relate to how communities are affected by changes in their environment and how they, in turn, influence their ecosystems (Laliberté et al. 2010, Valencia et al. 2015, Carmona et al. 2016, Santillán et al. 2019).

Functional traits, particularly when chosen well (Luck et al. 2012, Rosado et al. 2013, Lefcheck et al. 2015, Zhu et al. 2017), can be key indicators of ecosystem processes and community responses to environmental perturbations (Garnier et al. 2004). A very popular approach to analyzing relationships between ecosystem properties or community responses and environmental gradients involves the use of community

weight means (Lavorel and Garnier 2002). CWM of a trait is the average value of that trait calculated across all species in a community weighted by relative or absolute abundance, thus the word “weighted” (Lavorel et al. 2008, Lepš and de Bello 2023). This effectively makes CWMs single-dimensional counterparts of functional identity (Mouillot et al. 2013). Although the use of CWMs in community ecology is currently widespread and well-established, some studies questioned CWM analyses in studies of trait–environment relationships, claiming that this approach leads to overly optimistic results due to inflated type I errors (ter Braak 2019, Lepš and de Bello 2023). Nevertheless, CWM concept remains relevant mainly because it is an extremely simple and intuitive approach to study functional properties of communities and their change over time and environmental gradients (Lepš and de Bello 2023).

Functional diversity, unlike taxonomic diversity, aims to quantify the variation in functional traits across species within a community (de Bello et al. 2021b). Two communities with the same taxonomic diversity can have quite different functional diversity values, and vice versa (Devictor et al. 2010). The past two decades have seen a rapid development of methods for quantifying functional diversity of ecological communities (Schleuter et al. 2010, Mouchet et al. 2010, Chao et al. 2014, Carmona et al. 2016). Early studies in the field identified three main components of functional diversity: richness, evenness, and divergence (Mason et al. 2005b, Villéger et al. 2008a). These components relate to the volume of functional space occupied, how evenly species or biomass are distributed within this space, and how marginal species or abundances are located within this functional space, respectively (Mason et al. 2005b, Villéger et al. 2008a). (Mason et al. 2005b, Villéger et al. 2008b). Further studies have introduced indices measuring other dimensions of functional diversity, such as dispersion and redundancy, measuring how species are positioned with respect to each other in the functional space, or their distance to the centroid of the functional space (Laliberté and Legendre 2010, Mouillot et al. 2013, Ricotta et al. 2016, Pavoine and Ricotta 2019). Some of these indices have also been adapted to quantify dissimilarity between communities, serving as functional

counterparts to beta-level taxonomic diversity indices (Magurran and McGill 2011, Villéger et al. 2011, Carmona et al. 2016). Many of these indices have been successfully used to study consequences of changes in land use patterns and climate on functional properties of bird communities (Flynn et al. 2009, Weideman et al. 2020, Stewart et al. 2022).

Studying temporal changes in the taxonomic and functional composition of communities is essential for understanding and predicting outcomes of environmental perturbations on the maintenance of ecosystem functioning (Dornelas et al. 2014, Pérez-Ramos et al. 2017). Within this context, the concept of ecological stability, which refers to the ability of an ecosystem or community to maintain its structure and function over time, has become a central focus in ecological research over the past several decades (MacArthur 1955, Elton 1958, Pimm 1984, McCann 2000, Donohue et al. 2013). Ecological stability is a multifaceted and complex concept that encompasses various components (McCann 2000, Donohue et al. 2013). In simple terms, ecological stability can be defined as overall ability of an ecological system to remain in the same ecological state and to retain its function and structure in the face of perturbations (McCann 2000, Donohue et al. 2013). Numerous efforts have been made to define these components and develop methods to quantify them (Donohue et al. 2013). Earlier studies broadly categorized these components into two groups: those describing a system's ability to defy or resist the change and those describing its dynamic stability (MacArthur 1955, Holling 1973, McCann 2000). Components of stability that focus on a system's ability to defy change include resistance and resilience. Resistance measures the degree to which a variable changes after a disturbance (MacArthur 1955, McCann 2000), whereas resilience measures the time it takes for an ecological variable to return to its original or equilibrium state following a disturbance (Holling 1973, McCann 2000). Stability measures focusing on the dynamic stability features of ecological systems examine temporal variances in a community attribute, such as biomass, diversity, and composition (Pimm 1984, McCann 2000).

Considerable effort has been devoted to understanding the drivers of community stability, especially the effect of diversity (e.g., Cottingham et al., 2001; de Mazancourt et al., 2013; Ives & Carpenter, 2007; McCann, 2000). Various intrinsic attributes of a community can have a significant effect on the community stability. Most studies suggest that there is generally a positive relationship between biological diversity and ecological stability, though the relationship can be quite complex (May 1972, McCann 2000, Foster et al. 2002, Ives and Carpenter 2007, de Mazancourt et al. 2013a).

Several hypotheses have been proposed to explain the relationship between stability and diversity. These hypotheses can be grouped into four major categories (Figure 2.1; Cottingham et al., 2001; Johnson et al., 1996; McCann, 2000): the diversity-stability (complexity-stability) hypotheses (MacArthur 1955, Elton 1958), the rivet hypothesis (Ehrlich and Ehrlich 1981), the redundancy hypothesis (Walker 1992, Naeem 1998), and the idiosyncratic hypothesis (Lawton 1994).

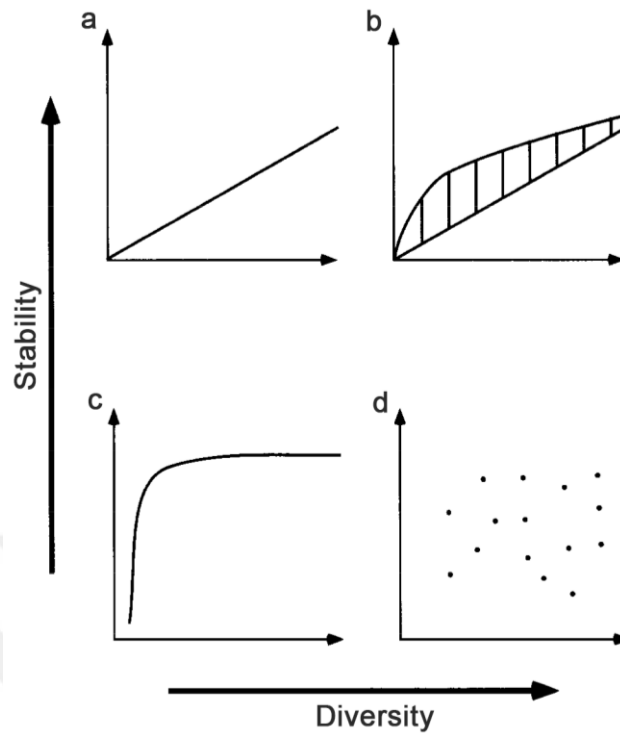


Figure 2.1 The four hypotheses about the role of diversity on stability of ecosystem processes: (a) the diversity-stability hypothesis, (b) the rivet hypothesis, (c) the redundancy hypothesis, and (d) the idiosyncratic hypothesis. Adapted and modified from Johnson et al. (1996).

The diversity-stability hypothesis suggests that as community diversity increases, the stability of an ecosystem process or a community attribute also increases (Figure 2.1a; Johnson et al., 1996; MacArthur, 1955). Explanations related to the underlying mechanisms are based on the assumption that higher number of interactions in diverse communities help in maintaining processes and resisting co-extinctions in case of declines (MacArthur 1955, Elton 1958, McNaughton 1977). Indeed, studies have found that species interactions, particularly resource-consumer interactions, are often quite weak across various taxa, including birds (Paine 1992, Goldwasser and Roughgarden 1993, Wootton 1997, McCann 2000). Other studies propose that the positive diversity-stability relationship may arise due to asynchronous responses of species within the community (Jiang et al. 2024), analogous to the concepts of functional compensation or functional complementarity (McNaughton 1977). The

diversity-stability hypothesis have been supported by a wide range of observational, empirical, and theoretical studies utilizing various stability components across multiple taxa, including birds (e.g., Carrara et al., 2015; Dell et al., 2019; Ding et al., 2013; Fowler, 2009; McGrady-Steed et al., 1997; Mikkelsen et al., 2011).

According to the rivet hypothesis, the removal or addition of species to a community has little impact after a certain threshold is crossed, after which it can lead to the collapse or realization of a given ecosystem or community process (Figure 2.1b; Ehrlich & Ehrlich, 1981). In this analogy, species function as “rivets” holding a structure together, and their loss beyond a certain point can cause a sudden breakdown (Johnson et al. 1996). This creates a nonlinear relationship between diversity and stability (Johnson et al. 1996). Still, in some communities, some species may be more influential or stronger “rivets” such as keystone predators and their removal can trigger the collapse of specific ecosystem or community functions (Estes et al. 2011).

The redundancy hypothesis proposes that species with similar functional properties can compensate for the loss of other species with similar roles (Figure 2.1c; Walker, 1992). Within these functional groups (Johnson et al. 1996) or groups of functionally-similar of species, loss of a few species can be compensated without noticeable change to the ecosystem process or community property of interest (Walker 1992, Naeem 1998). Lastly, according to the idiosyncratic hypothesis, the relationship between diversity and stability of an ecosystem process is unpredictable (Figure 2.1d; Lawton, 1994). This hypothesis suggest that there may no relationship between diversity of communities and stability of ecosystem processes or community properties, as the effects of species loss or addition can vary depending on context and specific ecological interactions (Lawton 1994).

I should note that concept of ecological stability discussed in this section of the introduction primarily relates to the stability of ecosystem functions rather than community stability, which is the main focus of this chapter. Community stability itself can be quantified in many different ways. Upon reviewing the literature on

community stability, I found that most studies quantify it as the inverse of change or variability in biomass or abundance (e.g., Carrara et al., 2015; Frost et al., 1995; Johnson et al., 1996; Lehman et al., 2000; Mikkelsen et al., 2011; Mönkkönen et al., 2017; Sadeghinia et al., 2023; Valencia et al., 2020; van Klink et al., 2019) or as change or variability in a single ecological function (e.g., Cardinale et al., 2011; Liu et al., 2013; Loreau & Hector, 2001; Pascoal et al., 2010; Tilman et al., 1996). Among these, some studies that focused on ecological functions, such as nutrient cycling or productivity, referred to the stability of these functions as “functional stability” (e.g., Pascoal et al., 2010). Others quantified functional stability by assessing changes within functional groups or number of functional, rather than focusing on a single function (Fischer et al. 2007, Van Looy et al. 2016, Smith et al. 2022).

Furthermore, some studies have recognized the multi-dimensional nature of functional stability and employed more complex methods (Lengyel and Botta-Dukát 2023). These studies often utilized a multidimensional hypervolume approach and quantified functional beta diversity as a measure of temporal functional stability (e.g., Leigh et al., 2019; Oliveira & dos Anjos, 2022). The same approach – using temporal beta diversity as a measure of community stability – has also been employed to quantify taxonomic or compositional stability of communities across various taxa including fish, invertebrates, plants, and birds (e.g., Huttunen et al., 2017; Mellin et al., 2014; Noon et al., 1985; Nunes et al., 2020; Oliveira & dos Anjos, 2022; Van Looy et al., 2016; Villéger et al., 2012; White et al., 2023). Other studies have taken alternative approaches to quantifying community stability (both compositional and functional) by focusing on different components of stability and community properties. For instance, some studies quantified temporal stability in community diversity, which they measured as both taxonomic and functional diversity (e.g., de la Riva et al., 2017; Pérez-Ramos et al., 2017).

At this point, I should clarify that I focused on the resistance component of community stability in this chapter of my thesis, as data were available from only two points in time, making studying dynamic stability impossible (Donohue et al.

2013, McCallum 2015). See section 2.2.8 for a detailed description of methods and approaches I used for quantifying community stability.

The stability of a community attributes can be shaped by its intrinsic properties of communities, such as their taxonomic or functional diversity (MacArthur 1955, Johnson et al. 1996, McCann 2000). According to the diversity-stability hypothesis, in general, as community diversity increases, the stability of an ecosystem process or a community attribute also increases (see above; Johnson et al., 1996; McCann, 2000). The effect of taxonomic diversity on community stability has been well documented (Carrara et al., 2015; Dell et al., 2019; Ding et al., 2013; Fowler, 2009; McGrady-Steed et al., 1997; Mikkelsen et al., 2011). Additionally, the functional structure and diversity of communities have been shown to influence multiple components of community stability across various taxa too (e.g., Carrara et al., 2015; da Silva et al., 2021; de la Riva et al., 2017; Ding et al., 2013; Leigh et al., 2019; Mikkelsen et al., 2011; Mönkkönen et al., 2017; Naeem & Li, 1997). Functional diversity, particularly when calculated using response traits, is considered an effective measure of a community's resistance and resilience to environmental perturbations (Elmqvist et al. 2003, Volaire et al. 2014). Some components of functional diversity, especially those that measure redundancy, have been studied in relation to bird community stability (Mikkelsen et al. 2011, Ding et al. 2013). However, these studies have not reached a consensus on the directionality of the relationship (e.g., Mönkkönen et al., 2017).

The stability of communities is also influenced by extrinsic factors, factors that are not inherent properties of communities. One such factor is the time gap between the consecutive sampling events or surveys. Time gap can be a key determinant of temporal stability of a community, simply because communities observed over shorter intervals are expected to exhibit higher similarity in taxonomic or functional composition (Lehman et al. 2000, Ives et al. 2003).

Another influential factor is the area itself. It is widely accepted that larger land surface areas typically offer larger patches of available habitats as well as a more

diverse collection of habitats. This, in turn, may support larger and more diverse communities that are better at resisting changes (MacArthur and Wilson 1967, Simberloff and Abele 1976, Whittaker and Fernandez-Palacios 2007).

Mean elevation of an area may also play a role in determining the stability of the communities it hosts. Given climate-driven elevational range shifts (e.g., Şekercioğlu et al., 2012), the resulting species turnovers, and the upward shift in distributional ranges of montane species, increasing geographic isolation between and among populations due to the finite dispersal capabilities of all organisms (La Sorte and Jetz 2010), it seems clear that mean elevation can influence community stability in multiple ways and directions. Furthermore, human impacts, including habitat degradation and land cover changes, tend to be more intense at lower elevations (Brooks et al. 2002, Körner 2004), but with some exceptions suggesting an inverse relationship for various reasons such as development of tourism (Price 1992). Therefore, the elevation at which a community is found has the potential to affect its stability.

The biome in which a community is located can also play an influential role in determining stability of the communities. Biomes on our planet have been facing different threats and undergoing distinct changes in their ecosystems (Sala et al. 2000, Ellis et al. 2010), suggesting that the communities within these biomes may also be changing at different rates over time.

The amount of protected area within a given patch can also influence the stability of the communities inhabiting it. Protected areas are central to conservation efforts (Coad et al. 2015, Cazalis et al. 2020, Santangeli et al. 2022). Although their conservation effectiveness depends on various factors, such as the degree of protection and management interventions (Coad et al. 2015, Cazalis et al. 2020), most protected areas are designed to conserve ecosystems and communities, thereby potentially contributing positively to stability of communities.

Land cover change is widely recognized as the most prominent driver of biodiversity loss and alterations in ecological communities globally (Sala et al. 2000, Jantz et al.

2015, IUCN 2022, Montràs-Janer et al. 2024). Although the intensity and nature of land cover change in Europe have varied over time and space (McNeill 2001, Ramankutty et al. 2006, Kuemmerle et al. 2016, Marques et al. 2019), studies have demonstrated that land cover change has consistently played a key role in shaping bird distributions over the last few decades (Murphy and Romanuk 2014, Keller et al. 2020, Soultan et al. 2022, Howard et al. 2023). This suggests that land cover change may be an important driver of bird community stability.

The temporal stability of ecological communities can also be influenced by the heterogeneity the habitat they are living in (Brown, 2007). Several studies have identified a positive relationship between landscape-scale habitat diversity and the temporal stability of bird communities, suggesting that a diverse set of habitats can support species with a diverse array of ecological strategies which in turn would weaken the concordance in response to environmental perturbations and enhance community stability (Hovick et al. 2015, García-Navas et al. 2021).

Climate change is considered one of the major drivers of compositional changes and stability in ecological communities (Huntley et al. 2008, Lawler et al. 2009, Gillings et al. 2015). Studies have shown that the bird populations are influenced by changes in temperature and precipitation, with the strength and direction of these effects depending on the habitat, species, and season considered (Sillett et al. 2000, Reif et al. 2010, Iknayan and Beissinger 2018, Fogarty et al. 2020). Numerous studies that documented shifts in bird distributions across various regions of the world (Thomas and Lennon 1999, Huntley et al. 2006, Jiguet et al. 2006, Murphy and Romanuk 2014, Gillings et al. 2015, Currie and Venne 2017, Howard et al. 2023). Some of these studies suggest that changes in climate tend to have weaker explanatory power for these shifts compared to more influential factors such as changes in land cover (Murphy and Romanuk 2014, Currie and Venne 2017, Howard et al. 2023). However, other studies indicate that climate change can be a major driver of observed and projected range shifts in birds (Lawler et al. 2009, Maggini et al. 2011, Hu et al. 2020). Regardless, it is clear that climate change should be considered

among the key factors influencing the stability of bird communities, particularly in analyses such as the one I intend to conduct in this chapter.

Dispersal refers to the movement of individuals from their birth sites to their breeding grounds or between successive breeding sites (Clobert 2012). Dispersal dynamics can play a significant role in determining taxonomic and functional structure as well as the stability of local communities (Weiher and Keddy 2001, Leibold et al. 2004, Scheiner and Willig 2011). The directionality and rate of dispersal can vary over time and depend on extrinsic factors such as climatic conditions, intrinsic factors like population demography and functional features of dispersers (Matias et al. 2013, Lu 2021, Garcia-R and Matzke 2021). Additionally, the outcome of a dispersal event (e.g., establishment or extinction) depends on various factors, including the relative strength of ecological processes acting at the local scale and ecological roles of the dispersing individuals (Weiher and Keddy 2001, Arumugam et al. 2021). Ultimately, dispersal apparently has the potential to influence community stability over time by regulating the flow of individuals between patches.

Knowing where species occur is essential for guiding conservation efforts and predicting ecological impacts of future environmental changes (Keller 2017). Large-scale atlas projects, which document the distributions of all species within a particular taxon, are particularly well-suited for these purposes (Gibbons et al. 2007, Keller 2017, Pototsky and Cresswell 2023). Such atlases have become the standard way for mapping bird distributions, driven by the growing popularity of birdwatching as a citizen science and resulting possibility of working together with a large number of volunteers (Gibbons et al. 2007, Pototsky and Cresswell 2023). By 2023, more than 600 bird atlases had been conducted across 93 countries, involving at least 380,000 participants involved (Pototsky and Cresswell 2023). These atlas studies have been valuable tools for ornithological studies, providing critical insights into long-term population trends, large-scale distributional changes, species-environment associations, and the identification of conservation-priority areas. Additionally, they provide raw data for investigating the drivers of distributional changes and developing predictive models, such as species distribution

models (Gibbons and Gates 1994, Donald and Fuller 1998, Fernández-García and Gainzarain 2004, Brotons et al. 2007, Keller et al. 2020, Soultan et al. 2022, Pototsky and Cresswell 2023, Howard et al. 2023).

2.1.2 Aims and objectives

This chapter of my thesis aims to uncover the effects of extrinsic factors (i.e., external environmental variables unrelated to the communities themselves) and intrinsic factors (i.e., inherent community properties, such as initial functional diversity) on the taxonomic and functional stability of breeding bird communities across Europe. To achieve this aim, I utilized data from two continental-scale breeding bird atlas from Europe that are conducted 30 years apart (Hagemeijer and Blair 1997, Keller et al. 2020) and analyzed changes in a wide range of environmental variables to identify the major extrinsic drivers of community stability. Additionally, I adopted a trait-based approach (de Bello et al. 2021b) and quantified species richness as well as various functional diversity metrics to assess how initial diversity influences temporal taxonomic and functional stability of communities. Since my dataset contains data from two time points, the stability component I focus on here aligns with the resistance or compositional turnover concepts (MacArthur 1955, McCann 2000, Donohue et al. 2013). Particular community properties I chose to study were taxonomic stability and functional stability, both of which I quantified using temporal beta diversity (Magurran and McGill 2011, Villéger et al. 2011).

2.1.3 Hypotheses

Below, I have listed my hypotheses for each of the variables tested and some of their interactions.

2.1.3.1 Trait community weighted means

As discussed in Chapter 1 of this thesis, previous studies have documented higher extinction rates in larger-bodied animals due to various factors, including the lower reproductive rate and output (Gaston and Blackburn 1995), tendency to intensive hunting or overexploitation (Whytock et al. 2016, Ripple et al. 2017), the thermoregulatory disadvantage of having large body in a warming climate (Gardner et al. 2011). Therefore, I hypothesized widespread declines in average body mass across the study communities.

I hypothesized overall increases in average relative brain mass values within the study communities. This hypothesis is based on the findings that higher relative brain mass in birds has been associated with higher population stability and an enhanced ability to cope with novel environmental conditions in our rapidly changing (Sol et al. 2005, Fristoe et al. 2017). Furthermore, a common type of land use change in my study region over the study period, increases in urbanization (Kuemmerle et al. 2016), is also known to favor larger-brained birds (Sol et al. 2020). Consequently, I expect widespread increases in brain mass across the study region.

The Earth's insect fauna seems to be going through a major collapse (van der Sluijs 2020, Wagner et al. 2021), which appears to negatively affect populations of insectivorous birds (Bowler et al. 2019, Tallamy and Shriver 2021). Therefore, I hypothesized overall declines in proportion of invertebrates in diet due to the loss of species that rely heavily on insect prey during their breeding season.

Previous studies have demonstrated that Europe has lost significant amounts of grassland habitat over the past several decades and that the remaining grasslands face heavy degradation (Cremene et al. 2005, Török et al. 2017, Pazúr et al. 2024). As a result, declines have also been observed in birds inhabiting these fragile habitats (Brennan and Kuvlesky Jr. 2005, Özgencil et al. 2021). For this reason, I expect widespread declines in CWM of the grassland trait across the study area.

2.1.3.2 Intrinsic factors

Given the overall positive relationship between diversity and stability (section 2.1.1), I hypothesized that grid squares with higher initial species richness would exhibit greater compositional stability. This expectation is based on the assumption that factors such as the dominance of weaker interactions and a greater number of trophic interactions contribute to the compositional stability of these communities (McCann 2000, Ives and Carpenter 2007, Donohue et al. 2013, de Mazancourt et al. 2013a).

My hypotheses regarding the effect of functional diversity of communities fall into two broad categories: those addressing the effect of a single component of functional diversity and those addressing the effect of multiple components simultaneously. The latter reflects my perspective that certain combinations of functional diversity metric values may create either a “deadly cocktail” or “invincibility cocktail”, rendering the community functionally less or more stable, respectively. In the following paragraphs, I elaborate on these two groups of hypotheses.

I propose several hypothesis focusing on individual components of functional diversity. Firstly, I hypothesize that the communities with higher functional redundancy will have higher stability. This one is probably the most intuitive hypothesis, as higher values of functional redundancy imply that there are species within a community with similar functional traits (Walker 1992, Ricotta et al. 2016). This high redundancy in terms of functional traits means that, when a species is lost, there will more likely be some functionally similar species that will keep the functional hypervolume more stable. The effect of species additions, however, is harder to predict. While the introduction of species with functionally unique traits could inflate FRic and decrease calculated stability, it is more probable that the new colonizers will be functionally similar to the ones already present in the community. This is because redundancy may result from environmental filtering, allowing for persistence of species with certain functional properties (Spasojevic et al. 2014, Özgencil et al. 2020). Furthermore, the functional redundancy metrics used in this thesis (see section 2.2.9.1) are designed to be independent of the trait volume

occupied (Ricotta et al. 2016, Pavoine and Ricotta 2019). While I do not rule out the possibility of new niche formation due to, for example, land cover change that can enable the establishment of functionally distinct species (Lavorel et al. 2011, Cadotte et al. 2011, Carmona et al. 2016), I simply consider the likelihood of functionally similar colonizers to be higher. Therefore, I suggest a positive relationship between functional redundancy and community stability.

Secondly, I hypothesize a unimodal relationship between FDis and functional stability. In my view, communities with very low or very high FDis are likely to experience higher turnover due to lack of redundancy or high sensitivity to disturbances, assuming functional trait values influence their responses (Elmqvist et al. 2003, Hordley et al. 2021). In contrast, I would expect communities with intermediate levels of FDis to exhibit the greatest temporal stability, simply because they would have a sufficiently diverse range of functional traits to enhance their resistance to environmental fluctuations and some level of redundancy to compensate functional changes caused by species turnover (Biggs et al. 2020, Hordley et al. 2021).

Third, I expect higher values of initial FDiv to render communities functionally less stable. This is because, a high FDiv value points to the presence of species near or on the periphery of the functional space occupied by community (Villéger et al. 2008a, Mouchet et al. 2010). This implies that, if a species is lost, it will more likely be one of the on the periphery and its loss will alter the convex hull of the community. Therefore, I hypothesize that FDiv would have a negative influence on temporal functional stability of the study communities.

Lastly, I hypothesize that FRic has no direct effect on functional stability of the communities. FRic measures the convex hull volume occupied by a community in functional space but does not confer detailed information about the relative positioning of individual species within the trait space (Cornwell et al. 2006, Villéger et al. 2008a). For this reason, I do not expect FRic alone to influence functional stability. Nonetheless, I chose to include this hypothesis because I suggest in

following paragraphs that FRic might impact community stability in combination with other metrics.

FOri and FSpe are unlike other metrics tested here, because community-level FOr and FSpe are calculated with reference to the species present in a larger species pool (Bellwood et al. 2005, Mouillot et al. 2013), which I defined as the collection of species in the entire dataset, comprising data from both EBBA1 and EBBA2 and covering the whole study area. As a result, FOr and FSpe values of a community are influenced by species that are not found within the community itself. This prevents these indices from being true “intrinsic” properties of communities and make them relevant only at the scale of the whole study area. My hypotheses regarding FOr and FSpe take this important characteristic into account. Specifically, I hypothesize that communities with high levels of FOr, indicating a high degree of isolation due to the presence of highly unique species, would have lower functional stability. In communities with high community-level FOr, species are less likely to have functionally similar counterparts. As a consequence, the addition or loss of a species is expected to cause a relatively large change in the convex hull volume. This hypothesis makes sense from a more ecological perspective as well. Previous studies have suggested that loss of functionally original species is common phenomenon in bird communities (e.g., Devictor et al., 2008; Liang et al., 2019 - also see Chapter 1 on this thesis).

High values of community-level FSpe indicate the presence of species located at the edges of the functional space occupied by the entire species pool. I expect FSpe to have no direct impact on functional stability of the communities, because this index does not provide any information on the exact positioning of species within the functional space with respect to other species in the same community.

In my view, certain combinations of certain functional diversity components can influence a community’s temporal functional stability. In the following paragraphs, I present my perspective on these combinations, which I refer to as “deadly cocktails” and “invincibility cocktails.”

First, I hypothesize that a combination of high FRic and high functional redundancy would enhance community stability beyond the effects of redundancy alone. A high value of FRic indicates that the community is made up of species with diverse functional properties, making it more adaptable to environmental changes (Mason et al. 2005b). Furthermore, it would make it more likely that a new colonizer will already fall inside, or at least not too far from, the large hypervolume occupied by the community, leading to minimal changes in the trait hypervolume. This, in my opinion, when combined with high redundancy, can create what I consider an “invincibility cocktail” for community stability.

Second, I expect communities with high FDis and high FNND to be less stable. This scenario reflects a community where species are functionally isolated from each other and positioned far from the centroid of the occupied functional space (Laliberté and Legendre 2010). Under these conditions, loss of a species can result in significant changes to the occupied trait hypervolume. The effect of colonizers is, once again, harder to predict, as it depends on various factors such as the relative strengths of the assembly forces in action and functional properties of the colonizing species. However, the aforementioned scenario might also indicate dominance of competitive forces, and if that truly is the case, new species additions are likely to maintain high FNND, leading to further modifications of the hypervolume and decreased stability.

Third, I expect communities with high FDiv and low functional redundancy to exhibit reduced temporal functional stability. In this scenario, the community consists of species with extreme trait values (high FDiv) that are concentrated at the edges of the functional space, but there is low redundancy to compensate for the loss of those extreme traits. Consequently, loss of a species at the edge of the functional space could drastically change the occupied hypervolume. Once again, predicting the impact of new colonizers is not so straightforward. However, if competitive forces are effective in community assembly, then I expect new species to have distinct trait values. In that case, species additions are also expected to cause profound changes in the occupied hypervolume, which would imply lower stability.

In summary, I hypothesize that low redundancy amplifies the destabilizing effects of high FDiv.

Finally, I propose that communities with high FEve and low FNND would likely remain more stable over time. High values of FEve indicate a more even positioning of species within the occupied functional space (Mason et al. 2005b, Mouillot et al. 2005). This may render the community's functional hypervolume more stable because any species loss or addition will more likely be in a region that is already "covered". From a more ecological and less methodological or formalistic perspective, higher FEve also promotes optimal resource use through complementarity, further enhancing stability (Mouillot et al. 2005, Wittebolle et al. 2009). Low FNND indicates that each species in the community has at least one close neighbor in functional space. This, when coupled with high FEve, can theoretically render a community functionally more stable.

I used interaction terms in my statistical models to represent these sets of conditions involving multiple facets of functional diversity. See section 2.2.10 for the details of the modeling approach I used to test the impact of these variables and their combinations.

2.1.3.3 Extrinsic factors

I proposed separate hypotheses for the extrinsic variables that I considered in my analyses. First, I hypothesized that squares with shorter time gap between surveys and larger land surface area should remain taxonomically and functionally more stable.

Second, I suggested that mean elevation should not be a significant determinant of community stability owing to balancing effects of the high species turnover resulting from upward elevational range shifts and extinctions happening due to the squeezing and isolation effects at higher elevations (Tingley and Beissinger 2013) and the lower levels of human impact at these elevations (Brooks et al. 2002, Körner 2004).

Third, it has been demonstrated that the prevalence and potential impact of each type of stressor in a biome can vary substantially (Myers et al. 2000, Sala et al. 2000), and there have been studies suggesting that the grassland and Mediterranean biomes may be the most affected and most vulnerable biomes in my study area (e.g., Cremene et al., 2005; Habel et al., 2013; Sala et al., 2000; Török et al., 2017; Underwood et al., 2009). Therefore, I hypothesized that the effect of having a high percent coverage of grassland and/or Mediterranean biome would negatively affect the temporal stability of breeding bird communities in my study area.

Fourth, my hypothesis regarding the effect of land cover change was straightforward and intuitive: The squares that experienced fewer land cover pixel changes over the study period should remain taxonomically and functionally more stable over time. As for the effect of initial land cover diversity, there were no studies that examined the relationship between initial land cover diversity and community stability and quantified community stability the way it is defined in this study (see section 2.2.8). Given this lack of the literature, I had to formulate a rather uninformed hypothesis. I will use a hypothetical example to explain the hypothesis that I propose. Consider two squares with the same surface areas but different land cover diversity values of $2H$ and H (Figure 2.2).

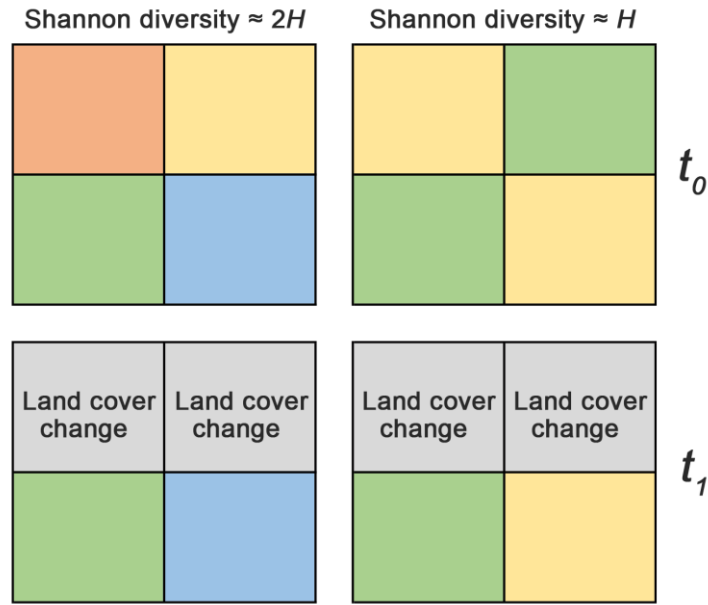


Figure 2.2 A hypothetical example demonstrating land cover change in two squares with different initial land cover classes. Colors represent different land cover classes.

In this hypothetical scenario, the square with the higher initial land cover diversity value would contain a greater variety of land cover classes (the square on the left hand side, at time = t_0) compared to the one with lower land cover diversity (the square on the right hand side, at time = t_0). These squares can also be imagined as alternative initial states of the same square. Now, suppose a land conversion occurs, where some portion of the land in the squares is transformed into different land cover classes (the two squares at time = t_1). I simulated such cases of land cover changes in R and calculated temporal taxonomic beta diversity (Sørensen's dissimilarity; Magurran & McGill, 2011; section 2.2.8) or β_{SOR} , using the *beta.pair* function in *betapart* package to compare the stability of the squares.

In my simple simulations, which I designed to help me develop my hypothesis, I assumed that each land cover class supports two species not found in other land cover classes, with a total of four different possible land cover classes. As shown in Figure 2.2, one of the squares contained all four different land cover classes, while the other had only two types. I then ran simulations where one, two, or three pixels experience

random land cover change and quantified β_{SOR} for each run. The number of simulations I ran was 100 for each case, which exceed the number of possible scenarios (i.e., $\binom{4}{1}, \binom{4}{2}, \binom{4}{3}$ - with even fewer combinations possible for the square with only two land cover types) .

In each of these simulations, the square with the higher initial land cover diversity exhibited higher taxonomic stability ($\sim$ overall 1.5-2 times smaller β_{SOR}). I acknowledge that this a highly simplified set of simulations, as there may be species that occur in more than one land cover type, such as some generalist corvids (Madge and Burn 1994), and land cover classes may differ in terms of the number of species they can support. All of these would have a significant impact on the outcome of the simulations, but I, once again, chose a simpler approach and went with basic simulations to help me form my hypothesis.

Ultimately, considering the simulations results, I hypothesized that the squares with high initial land cover diversity should have higher temporal taxonomic stability compared to squares with relatively lower initial land cover diversity. On the other hand, I expect the initial land cover diversity to have a negligible effect on functional stability. This is because, I expect the nature of the land cover transformation, rather than the initial land cover diversity, to determine the set of functional traits the colonizers and extinct species would bear. For instance, a change from forest to grassland would have a more profound impact on change in trait volume occupied by a community (Villéger et al. 2008a) than a change from forest to shrubland, which is expected to be structurally and ecologically more similar to forest than grassland. Consequently, I would expect a greater overlap in the trait or niche volume occupied by the species of forests and shrubland compared to species of forests and grassland, as structurally and ecologically more similar habitats are expected to support communities of species with similar trait values (Weiher et al. 1998, Cornelissen et al. 2003, Jetz et al. 2012).

Finally, I hypothesized that the proportion of protected areas present in a square would positively impact the stability of communities inhabiting it, thanks to an overall lower human impact in such areas (Coad et al. 2015, Cazalis et al. 2020).

2.2 Material and methods

2.2.1 Study area

The study area included westernmost parts of Eurasia, continental Europe, the Mediterranean Islands, the UK, and Iceland. Even after the geographic filtering, the final dataset spanned an astonishing 5.3 million km². In this section, I explain the filtering procedure and present the study area.

2.2.1.1 Geographic and temporal filtering of the atlas datasets

I conducted the geographical and temporal filtering of the EBBA1 and EBBA2 datasets in two steps. The first step involved the removing the squares that were surveyed only in one of the atlases but not the other. There were many such squares from across Europe and Eurasia. For example, the Thracian or European Türkiye was the only part of Türkiye that was surveyed for EBBA1 (Hagemeijer and Blair 1997), whereas many squares from across the entire country were surveyed for EBBA2 (Keller et al. 2020). Additionally, the Greek islands in the Aegean Sea were surveyed during EBBA1, while the Turkish islands were not (Hagemeijer and Blair 1997, Keller et al. 2020). Therefore, I excluded the squares encompassing both European Türkiye and Asia Minor (e.g., those in the Dardanelles or Bosphorus) and the squares encompassing both Greece and Asia Minor. There was also a single square located at the Gibraltar that had land significant amounts of land both in Iberia and North Africa. I excluded this square from my analyses simply because no breeding bird atlas surveys were conducted in Morocco during EBBA1 and EBBA2. The second step of the geographical filtering considered the temporal span of data

collection for each country and the data collection methods used. The time gap in between two consecutive surveys is expected to be an important determinant of taxonomic and functional stability of communities (Legendre and Gauthier 2014). Although I included time gap between EBBA1 and EBBA2 for each square as a covariate in my analyses to account for any potential effect it can have on community stability (see section 2.2.9.2.1), I still opted to exclude Russia from my analyses due to its extremely long data collection period (Table 2.2 and 2.3). I made this decision because data collection periods that are even longer than the average time gap between EBBA1 and EBBA2 (~30 years) could easily jeopardize the entire analyses. I included Norway in my analyses, although its EBBA1 survey data collection took place between 50-89 (and 94). This decision was based on the fairly low volume of the data from outside the main data collection window of 1985-1989 (Hagemeyer and Blair 1997) and the example set by other published studies that used EBBA1 and EBBA2, which included data from Norway in their analyses without encountering any issues, while excluding data from Russia (e.g., Howard et al., 2023; Soultan et al., 2022). I also excluded data from countries where the only data collection methods used were records from local studies and visitors, rather than direct and targeted atlas surveys. In the end, I had to exclude Russia (including Kaliningrad), Georgia, and Armenia, as well as all squares having land in these countries, from my study for the reasons listed above.

I further removed squares with incomparable sampling effort in the two atlases to control for any bias resulting from the variation in sampling effort following (Keller et al. 2020, Howard et al. 2023). I did not conduct any further geographical or temporal filtering to keep my sample size (i.e., number of study squares) as high as possible.

In the end, I ended up with a total of 2,070 study squares after excluding squares 2,078 squares for the reasons outlined above. Maps of the 50 km x 50 km UTM squares that were included in the study and those that were excluded are given below in Figure 2.3. I used the *ggplot2* package (Wickham et al. 2016) to visualize all maps and plots in this section.

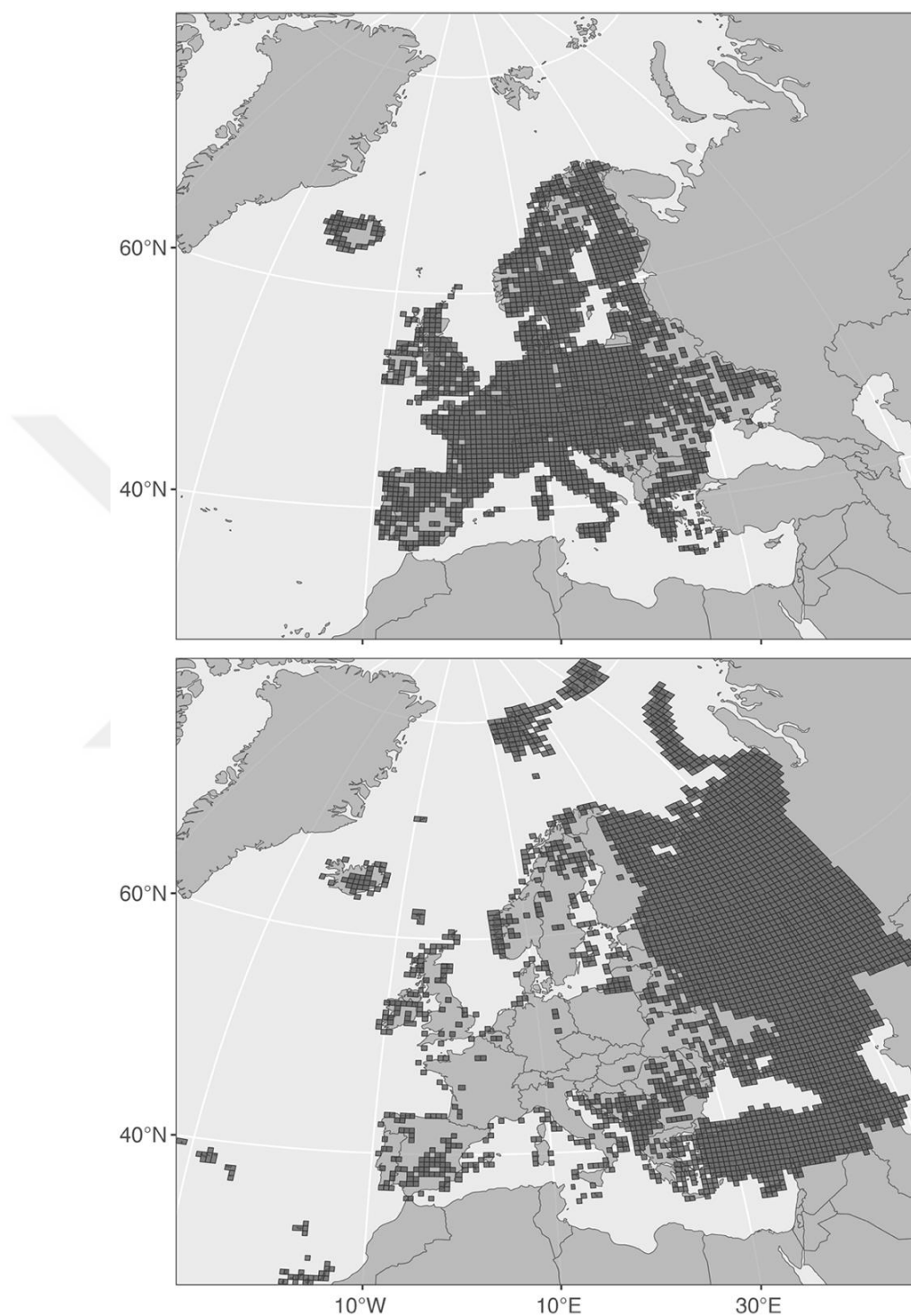


Figure 2.3 50 km x 50 km atlas squares included in the study (upper) and excluded from the study (lower). See above for a detailed description of the filtering process.

2.2.1.2 Geographic extent of the study area

The final study area spanned a huge latitudinal ([34.8, 71.2] - nearly 36.4 degrees) and longitudinal ([-24.9, 39.7] - nearly 64.5 degrees) range and covered an astonishing 5.3 million square kilometers, which I calculated by transforming the study area layer to the Mollweide projection (EPSG:54009), an equal-area projection suitable for area calculation in areas that are as large as my study area (Hager 1988, Kimerling et al. 2016), by using the utilities of the *sf* package (Pebesma 2018) in R (R Core Team 2024). The study area encompasses political boundaries of 39 countries/autonomous regions. These were Austria, Åland Islands, Bosnia and Herzegovina, Belgium, Bulgaria, Belarus, Switzerland, Czech Republic, Germany, Denmark, Estonia, Spain, Finland, France, United Kingdom, Guernsey, Greece, Croatia, Hungary, Ireland, Isle of Man, Iceland, Italy, Lithuania, Latvia, Moldova, Montenegro, North Macedonia, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Sweden, Slovenia, Slovakia, Türkiye, and Ukraine (Figure 2.3).

2.2.1.3 Mean temperature and total annual precipitation in the study area

The extensive geographical range of the study area results in a wide range of climatic conditions. I used the WorldClim database version 2.1 historical climate data (Fick and Hijmans 2017) to obtain average monthly temperature and total monthly precipitation data for the study area. This dataset uses the average climatic values for the 1970-2000 period (Fick and Hijmans 2017). Using the second highest available spatial resolution of approximately 4.63-km or 2.5 arc minutes, I calculated the annual mean temperature and total annual precipitation (Figure 2.4 and 2.5).

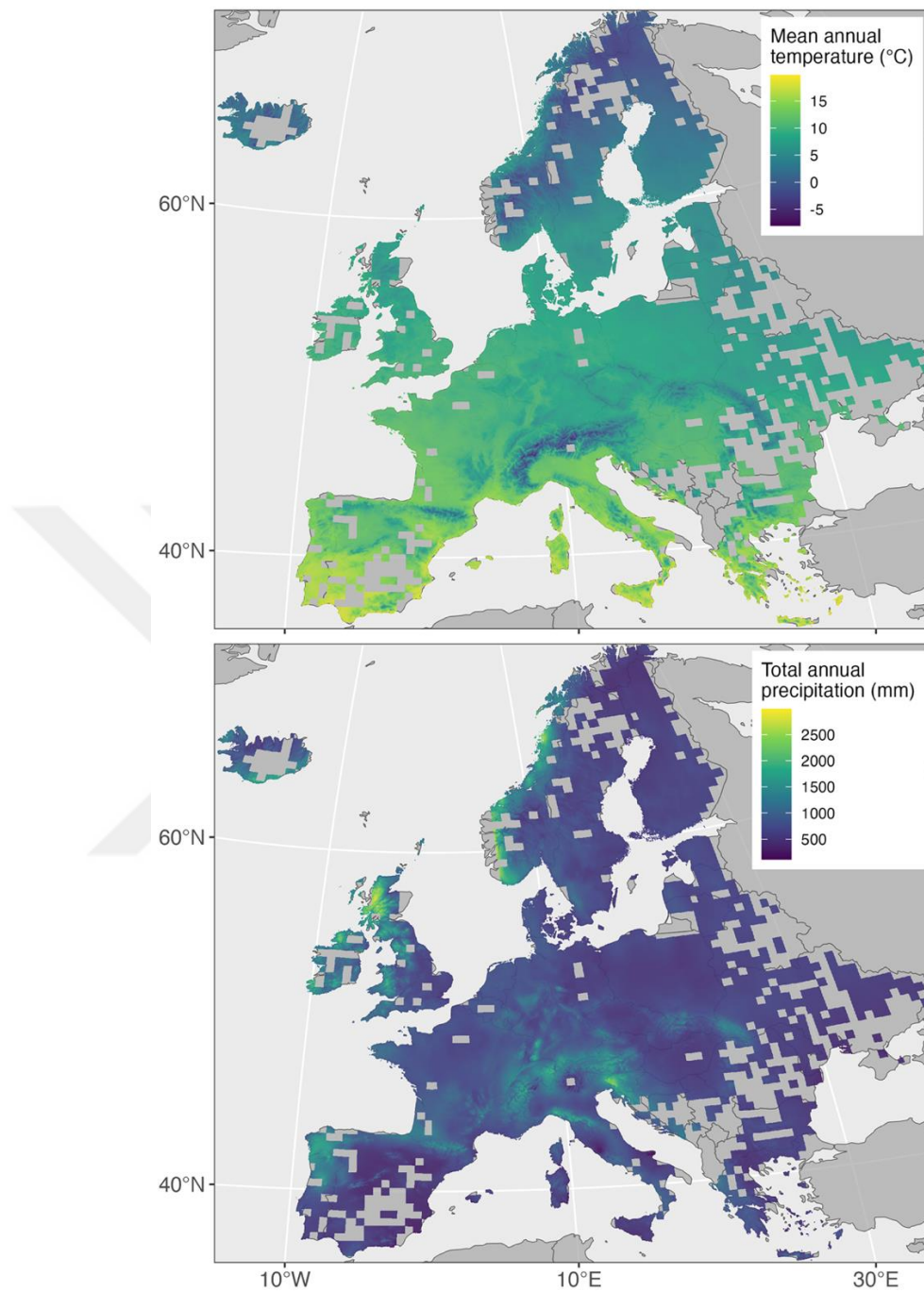


Figure 2.4 Mean annual temperature in the study area (upper) and total annual precipitation (lower) in the study area. Source: Fick & Hijmans (2017).

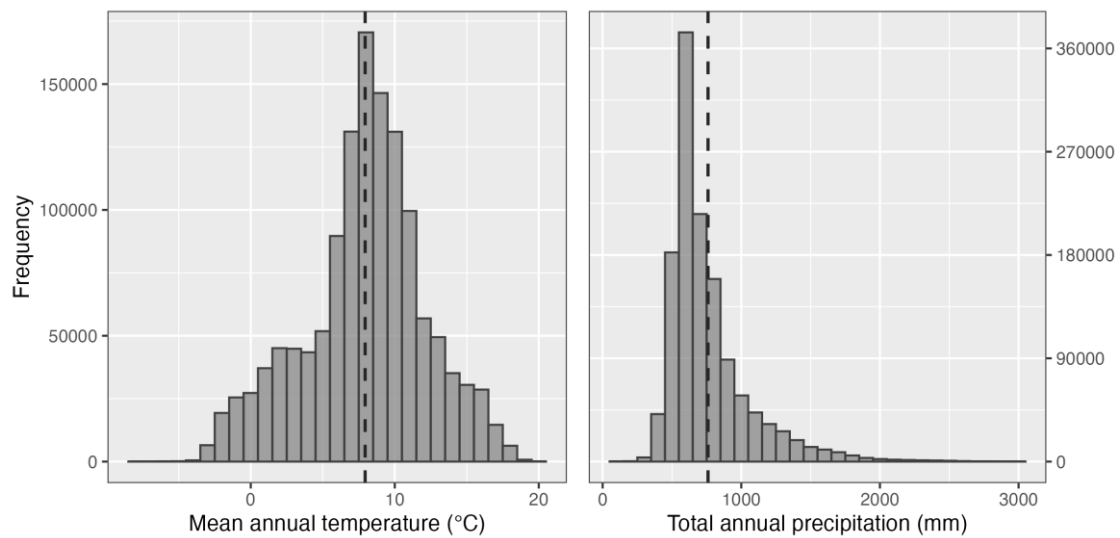


Figure 2.5 Mean (dashed lines) and distributional ranges of the mean annual temperature (left) and total annual precipitation (right) in the study area. Source: Fick & Hijmans (2017).

Based on the WorldClim historical climate dataset, the mean annual temperature in the study area is 7.93 °C, ranging from -8.01 to 19.79 °C (Figure 2.5a). The total annual precipitation has a mean of 760.16 mm and ranges between 111.13 and 2,991.47 mm (Figure 2.5b).

2.2.1.4 Elevation in the study area

To provide an overview of the elevation profile of the study area, I downloaded GTOPO30: Global 30 Arc-Second Digital Elevation Model (USGS 1996) and cropped it using the extent of the study area in Google Earth Engine (Gorelick et al. 2017). The cropped digital elevation model is shown in Figure 2.6. The data used in this visualization is aggregated by a factor of five, meaning the data is at approximately 5x5 km spatial resolution. I also calculated the mean and range of data using the high, untransformed data, finding that the mean elevation in the study area is approximately 293 m.a.s.l., and the elevation ranges from -5.5 m.b.s.l. to a maximum of approximately 4,390 m.a.s.l. in the Alps.

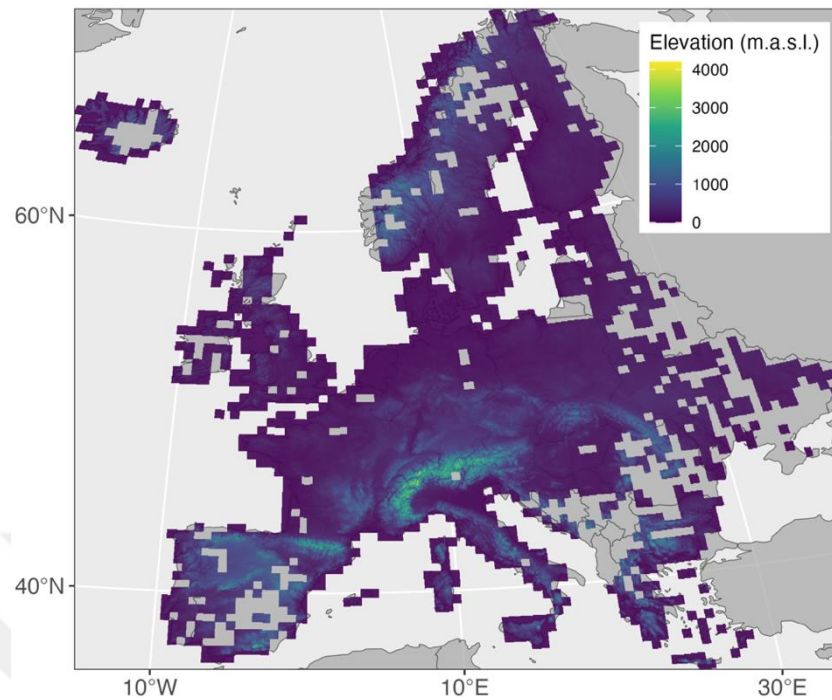


Figure 2.6 Elevation map of the study area. Source: USGS (1996).

2.2.1.5 Biomes of the study area

In order to present an overview of the biogeographical regions in my study area, I utilized the widely-used Olson et al. (2001)'s global biomes map, available in a high-resolution vector format at <https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world>, and processed it present in R using the *sf* package. After I cropped the global biomes map, I found that my study area encompassed six different biomes: temperate broadleaf & mixed forests (58.8% of the total area), temperate conifer forests (6.1%), boreal forests (13.8%), temperate grasslands, savannas & shrublands (2.4%), tundra (3.5% of the total area), and Mediterranean forests, woodlands & scrub (13.4% of the total area). Map of the biomes present in my study area is given in Figure 2.7.

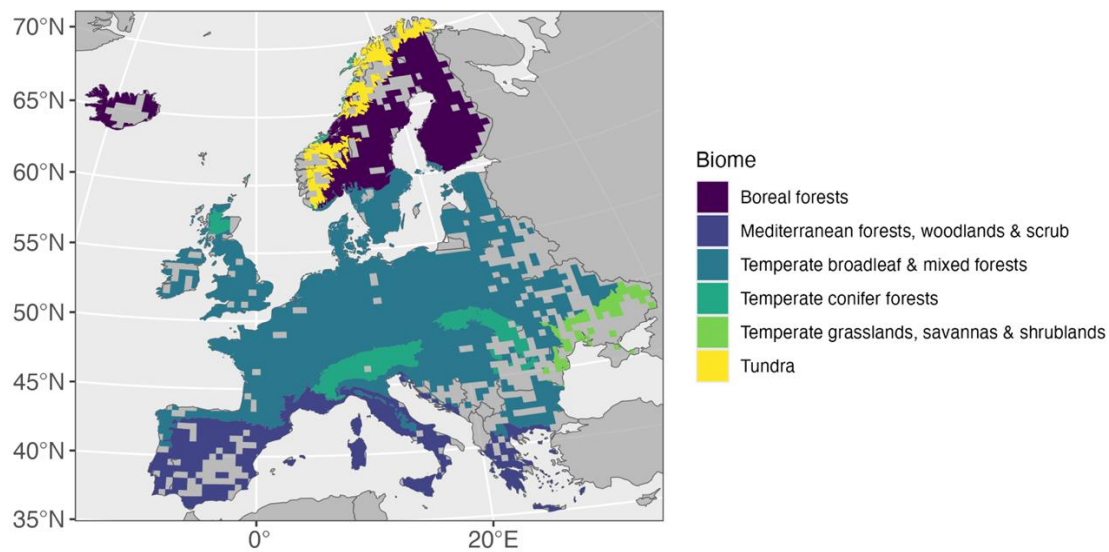


Figure 2.7 Biomes found within the study area. See Olson et al. (2001) for a detailed description of these biomes.

2.2.2 Breeding bird atlases

I utilized two continental-scale breeding bird atlases separated by approximately 30 years to identify factors that influence taxonomic and functional stability of breeding bird communities in Europe.

2.2.2.1 The EBCC Atlas of European Breeding Birds 1997 (EBBA1)

European Bird Census Council (EBCC) coordinated a cross-continental breeding bird atlas in the 1980s (Hagemeijer and Blair 1997). The area covered by the atlas spanned 45 countries/autonomous regions with respect to current political boundaries. The original atlas was meant to take place during 1985-1988, and the participating nations planned their own fieldwork schedule, but because of practical difficulties, many of the national atlas teams failed to meet the timescale. This resulted in a temporally heterogeneous data collection process.

The national atlas teams would ideally adopt identical methods to collect species distribution data, but in the case of this atlas, it was not possible. Therefore, the coordinators of the project issued wide-ranging guidelines instead. In the end, the atlas teams employed various field methods including single visits, multiple visits, and systematic surveys based on line transects, point transects, or territory mapping (Bibby et al. 2000, Buckland et al. 2001). In some of the countries, the atlas study was combined with national-scale studies, whereas in some others, the teams conducted independent fieldwork exclusively for EBBA1. In addition to the presence/absence data collected, the field crews also collected information on the level of breeding evidence by utilizing a set of standardized breeding categories or breeding codes. There are a total of 16 of these breeding codes, and they are divided into three major categories: A for possible breeding evidence, B for probable breeding evidence, and C for confirmed breeding evidence (Table 2.1; Greenwood, 2017; Hagemeijer & Blair, 1997). These breeding codes are indicative of likelihood a that a bird species is breeding in an area. The same breeding codes were also used in European Breeding Bird Atlas 2 (section 2.2.2.2). In the end, by using all the breeding evidence data collected on the study species, the researchers then assigned the highest breeding code obtained to each species in each square they occur. The breeding codes used in EBBA1 and EBBA2 are given in Table 2.1.

Table 2.1 Breeding categories or codes used in The EBCC Atlas of European Breeding Birds 1997 (EBBA1) and European Breeding Bird Atlas 2 (EBBA2).

A: Possible breeding

A1 Species observed in breeding season in possible nesting habitat

A2 Singing male(s) present (or breeding calls heard) in breeding season

B: Probable breeding

B3 Pair observed in suitable nesting habitat in breeding season

B4 Permanent territory presumed through registration of territorial behaviour

B5 Courtship and display

B6 Visiting probable nest site

B7 Agitated behaviour or anxiety calls from adults

B8 Brood patch on adult examined in the hand

B9 Nest building or excavating of nest hole

C: Confirmed breeding

C10 Distraction display or injury feigning

C11 Used nest or eggshells found (occupied or laid within period of survey)

C12 Recently fledged young or downy young

C13 Adults entering or leaving nest site in circumstances indicating occupied nest

C14 Adult carrying a fecal sac or food for young

C15 Nests containing eggs

C16 Nests with young seen or heard

In the end, EBBA1 resulted in collection of data on presence of a total 495 species across its study area. Table 2.2 gives the list of the participating countries, their data collection periods, and general strategies used to collate the data. For more information on EBBA1 see Hagemeijer & Blair (1997). I downloaded the whole EBBA1 from the Global Biodiversity Information Facility's (GBIF) website (GBIF.org), where the dataset was freely available (Hagemeyer et al. 2016).

Table 2.2 Countries/autonomous regions that participated in the EBCC Atlas of European Breeding Birds (EBBA1), their data collection periods and methods. Source: Hagemeijer and Blair, (1997). DR= Direct recording, LR= Local records, VR= Visitors records, *excluded countries.

<i>Country/Autonomous region</i>	<i>Data collection period</i>	<i>Main source of data</i>
Albania	85-93	DR, LR, VR
Armenia*	85-93	LR
Austria	85-88	DR
Azerbaijan*	94	LR, VR
Azores	82-95	DR
Belarus	72-92	DR
Belgium	85-89	DR
Bulgaria	80-89	DR
Czechia	85-88	DR
Croatia	85-88	DR
Denmark	85-88	DR
Estonia	85-88	DR
Faroese	81-89	DR
Finland	86-90	DR
France	80-92	DR, LR
Georgia	92	VR
Germany	79-90	DR
Great Britain	85-88	DR
Greece	81-90	VR
Hungary	79-91	DR
Iceland	85-95	DR
Ireland	85-88	DR
Italy	79-82	DR, LR
Latvia	85-88	DR
Lithuania	85-88	DR
Luxembourg	76-90	DR
Madeira	85-95	DR
Malta	85-88	DR
Moldova	86-90	DR
Norway	50-89	DR
Poland	86-93	DR
Portugal	78-89	DR
Romania	77-92	DR
Russia*	63-94	LR, DR, VR
Slovakia	85-88	DR
Slovenia	79-88	DR
Spain	70-92	DR, LR
Sweden	86-91	DR
The Netherlands	84-90	DR
Switzerland	85-88	DR
Türkiye (Thrace)	88-95	DR
Ukraine	80-93	DR, LR, VR
Ex-Yugoslavia	85-92	DR, LR

2.2.2.2 European Breeding Bird Atlas 2 (EBBA2)

EBCC organized a second breeding bird atlas covering a vast area ranging from the Urals to the Canary Islands (Keller et al. 2020). The final study area spanned more than 11 million km², corresponding to nearly 7% of the world's emergent land. Fieldwork for the atlas took place between 2011 and 2018, with most it happening between 2013 and 2017. Table 2.3 provides a list of participating countries, their data collection periods, percentage of data collected in each period, and general strategies each country used to collect data.



Table 2.3 Countries/autonomous regions that participated in the European Breeding Bird Atlas 2 (EBBA2), their data collection periods, percentage of data collected in each period, and general strategies applied in data collection. Source: Keller et al., (2020). Tar = Targeted atlas surveys, Mon = Monitoring data, At = Regional atlas data, Cas = Casual observations, *excluded countries.

Country/Autonomous region	1991-2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	Main source of data
Albania															100%					Tar
Andorra															100%					Tar, Mon
Armenia*								20%							80%			20%		At
Austria															100%					At
Azerbaijan*	5%				5%						15%						40%	20%		Tar, Cas
Belarus										3%					92%		5%			Tar
Belgium															99%			1%		Tar, Mon, Cas
Bosnia & Herzegovina															100%					Tar
Bulgaria															100%					Tar, Mon
Croatia								1%							96%			3%		Mon, Tar, Cas
Cyprus*															100%					Tar, Mon, Cas
Czechia															100%					At
Denmark															100%					At
Estonia															100%					Tar, Mon, Cas
Faroes															100%					Cas
Finland							50%									50%				At, Mon, Cas
France													100%							At, Mon, Cas
Georgia															100%					Tar, Cas
Germany														100%						At, Mon, Cas
Greece				1%								1%			84%			15%		Tar, Mon
Hungary															100%					Mon, Cas
Iceland	15%					15%									70%					Mon, Cas
Ireland															100%					Mon, Cas
Italy															100%					At, Mon
Kazakhstan															100%					Tar
Kosovo															100%					Tar
Latvia															100%					At, Mon, Cas
Lichtenstein															100%					At
Lithuania															100%					Cas
Luxembourg															100%					Mon, Cas
Malta															100%					Cas
Moldova																100%				Tar
Montenegro															100%					Tar, Cas
North Macedonia							1%								99%					At, Mon, Cas
Norway										2%					98%					Mon, Cas
Poland	2%						4%								94%					Mon, Cas, Tar
Portugal											1%				99%					At
Romania															100%					Mon, Cas
Russia*								8%							87%			5%		At, Tar
Serbia															100%					At
Slovakia															100%					Mon, Cas
Slovenia							40%								60%					At
Spain															90%			10%		At, Mon, Cas
Sweden															100%					Cas, Mon
Switzerland															92%		8%			At, Mon, Cas
The Netherlands															88%		12%			At
Türkiye								29%							70%			1%		At
Ukraine															100%					Tar, Cas
United Kingdom															100%					Mon, Cas

The methodology used in data collection was determined by national partners with the support of experts. The data sources and collection methods varied among countries and included regional atlas data, monitoring data, casual observation, and targeted EBBA2 surveys (Table 2.3). This variation in data collection methods was not considered a limitation, as it allowed different situations in each country, such as total survey area, number of available experts, financial resource limitation, to be taken into account during sampling design and data collection. Furthermore, some common standards in data collection were established to ensure a high level of comparability.

EBBA2 also employed standardized timed surveys with multiple visits. During these surveys, which lasted for 60 to 120 minutes, the observers recorded all birds they heard or saw. These surveys were primarily meant for the species distribution models, which tend to produce more accurate output using data collected in a standard way compared to opportunistically collected data (Milanesi et al. 2017, Keller et al. 2020). Unlike EBBA1, EBBA2 also reported coarse abundance estimates (1-9, 10-99, 100-999, 1000-9999, 10000-99999, and >100000 pairs) for many species, which were made with the help of a set of standardized guidelines on how to conduct direct counts, expert assessment, and statistical inference to assess abundance for each atlas square (Keller et al. 2020).

As in EBBA1, data on breeding evidence was also collected using the same breeding codes listed in Table 2.1. By the end of EBBA2 data collection period, data on distributions and breeding evidence of a total of 569 species had been collected. For more information on EBBA2 see Keller et al. (2020). I requested and downloaded the EBBA2 occurrence dataset from EBBA2's official website (ebba2.info; EBCC, 2022; Keller et al., 2020). Unfortunately, my request for abundance data was denied by the EBCC. However, this was not entirely bad news, as it allowed me to use incidence data from both EBBA1 and EBBA2. This, in turn, provided a higher level of compatibility and more reliable inferences.

2.2.2.3 Breeding codes considered in the study

Breeding codes provide valuable information on breeding likelihood of species, but they are highly influenced by species-specific difficulty of obtaining a high breeding codes, variations and biases in sampling effort and geographical coverage (Keller et al. 2020). In my thesis, I used breeding records associated with all three major breeding categories (Table 2.1), which are possible, probable, and confirmed breeding (Hagemeijer and Blair 1997). This decision of mine was based on the idea that for some of the species, such as the reed-nesting passerines (Passeriformes), confirmed-coded records may be hard to get, possibly resulting in a bias in the dataset. I think a good portion of the records that are left with a maximum of A-category breeding codes (especially in low-effort areas) are indeed breeding in the areas where they were spotted, and it seems like these species' breeding codes stayed low only because of the difficulty of obtaining high breeding codes within some challenging habitats, their low population size, or because of their shy nature (Keller et al. 2020). Furthermore, over-summering individuals-migrants that remain in their wintering grounds during the breeding season for various reasons (Martínez-Curci et al. 2020, Aarif et al. 2020)- may not display behavior associated with the higher levels of breeding evidence. This does not mean that these individuals do not engage in any species-species interactions or contribute to ecosystem functions (Greenberg 1986). It simply indicates that they do not participate in reproduction-related activities, such as nest building or raising young, and hence do not have not have the specific needs associated with these activities. Nevertheless, the over-summering individuals are still part of the ecosystems and ecological networks in which they live (Greenberg 1986). Fortunately, many of these over-summering birds can be correctly identified as non-breeding by expert ornithologists and receive no breeding codes at all. Although they are not reproducing in the areas they are observed, I think it is perfectly appropriate to consider over-summering individuals- which typically receive A-coded breeding codes- as a part of the community, for the reasons I listed above.

There are many studies in the literature that considered breeding evidences from all levels of certainty, including the possible-coded ones, as a sign of breeding (Polakowska et al. 2012, Ma and Zhang 2015, Šímová et al. 2015, Soultan et al. 2022, Howard et al. 2023). Conversely, there are some other studies that opted to use only the probable and confirmed-coded records (e.g., Titeux et al., 2004; Venier et al., 2004). I acknowledge that this decision that I made poses a trade-off. On the one hand, being more inclusive may possibly generate a more complete breeding bird community, higher sample size, but some non-breeding species may be wrongly labelled as “breeding”. On the other hand, being more conservative and sticking with only the higher levels of breeding evidence may allow me to more reliably estimate true composition of the breeding bird communities, but this comes with the cost of lower sample size and exclusion of some breeding species that ended up with possible breeding codes only because of their cryptic nature or low population size. In this study, I chose to be more inclusive by including the possible-coded records alongside probable and confirmed ones, and my results should be viewed by keeping in mind the pros and cons of such an approach.

2.2.3 Focal taxa and taxonomic corrections

In this chapter of my thesis, I focused on breeding landbirds as well as inland wetland birds. Following sections describe the taxonomic treatments and species filtering I carried out.

2.2.3.1 The taxonomic code and taxonomic conversions

In this thesis, I used the Clements Checklist of Birds of the World v2023b (Clements et al. 2023), a comprehensive and widely-used bird taxonomy reference, which is also the taxonomic code adopted by the eBird platform. The particular update that I used was published in December 2023, and it is available on

<https://www.birds.cornell.edu/clementschecklist/introduction/updateindex/december-2023/> for download.

There was a number of changes to scientific names of the species as well as some taxonomic splits and a merge based on DNA data between the survey and publication periods of EBBA1 and EBBA2, and deciding on which species identity to use is crucial as it directly influences the results of spatial (by determining the spatial distribution) and trait-based (by determining the trait values used) analyses.

To deal with the taxonomic changes in a systematic way, I first detected the species that had different names in EBBA1 and EBBA2. Many of these nomenclatural differences arose from recent taxonomic splits based on molecular studies (see below). To be consistent in my approach, I came up with a guideline, presented in Table 2.4, for determining the appropriate scientific names and trait values for each taxa.

Table 2.4 Different cases of taxonomic changes and how they were treated.

<i>Taxonomic change</i>	<i>Decisions about naming and use of trait values</i>
Name change with no splits or merges	Use the most recent name and the species' trait values.
Split after EBBA1 with <u>more than one</u> daughter species distributed within the study area	Use a hybrid naming scheme for the taxa. Use either average trait values or the mother species' trait values depending on the relative sizes of the distributional ranges of the daughter species and data availability.
Split after EBBA1 with <u>only one</u> daughter species distributed within the study area	Use the most recent name of the daughter species that is found in the study area. Use the trait value for this species if available; if not, use the trait value of the mother species.
Merge after EBBA1 with <u>more than one</u> former species distributed within the study area	Use a hybrid naming scheme for the taxa. Use either average trait values or the new species' trait values depending on the relative sizes of the distributional ranges of the daughter species and data availability.

In cases where a species was simply renamed without undergoing any splits or merges, I opted to use the most up-to-date name from Clements v2023b. Splits were the most common type of taxonomic changes encountered in this study, and I treated the splits differently, based on the past and current distributions of the newly-defined daughter species and the availability of their functional trait data. A complete list of

the taxonomic changes made due to splits, along with the references used to investigate the systematic history of the species, is given in Table 2.5.

Table 2.5 Taxonomic changes made in the thesis as a result of taxonomic splits and the systematic history references used.

<i>Original scientific name in the dataset</i>	<i>Scientific name used in the study</i>	<i>Reference</i>
<i>Lanius meridionalis</i>	<i>Lanius excubitor</i>	Yosef et al. (2020)
<i>Curruca balearica</i>	<i>Curruca sarda</i>	Aymí and Gargallo (2021)
<i>Iduna opaca</i>	<i>Iduna pallida</i>	Svenson and Christie (2020)
<i>Phylloscopus orientalis</i>	<i>Phylloscopus bonelli</i>	Clement (2020a)
<i>Cyanopica cyanus</i>	<i>Cyanopica cooki</i>	Madge and de Juana (2020)
<i>Picus sharpei</i>	<i>Picus viridis</i>	del Hoyo et al. (2020)
<i>Carduelis corsicana</i>	<i>Carduelis citrinella</i>	Clement (2020b)
<i>Sylvia hortensis</i>	<i>Curruca crassirostris</i>	del Hoyo et al. (2021)
<i>Phylloscopus ibericus</i>	<i>Phylloscopus collybita</i>	Clement and Garcia (2020)
<i>Larus cachinnans</i>	<i>Larus argentatus</i>	Burger et al. (2020)
<i>Calandrella rufescens</i>	<i>Alaudala rufescens</i>	Alström et al. (2023)
<i>Corvus cornix</i>	<i>Corvus corone</i>	Madge (2020)
<i>Saxicola torquatus</i>	<i>Saxicola rubicola</i>	Collar (2020)

The most common type of splits involved cases where multiple daughter species, previously considered subspecies of the same species, are both present in the study area. For most of these splits, it was impossible to tell which (sub)species the EBBA1 presence/absence data referred to. In these cases, I defaulted to using the mother species' name and its trait values. One can argue that in cases where one of the daughter species is spatially isolated (e.g., island endemics) or has minimal range overlap with the other daughter species, it might be possible to determine which species the original EBBA1 dataset referred to. However, even in that case, there is still a risk of misinterpreting the original dataset, particularly in areas where range overlap is possible. Moreover, most of these new species lack designated trait values in the functional trait databases, as they were not recognized as species when these trait databases were published. Therefore, for such splits, I used the mother species' scientific name and its functional trait values. The second type of splits that I encountered were the ones where one of the daughter species is not found within the boundaries of the study area. In such instances, I used the newly-defined species' scientific name and its trait values. Once again, when the functional trait data was not available in the trait databases, I used the mother species' functional trait values.

After making all necessary corrections and conversions, the two datasets (i.e., EBBA1 and EBBA2 datasets) used in the study became compatible, enabling further analysis.

2.2.3.2 Excluded species and final species list

One of the main objectives of this thesis was to investigate the influence of various extrinsic factors on the temporal stability of breeding bird communities (section 2.2.9). Among these extrinsic factors are climatic variables, topography, and land cover, which are known to influence the distribution of many bird species (Milanesi et al. 2017). However, the distribution of exotic species, either traded or invasive, is often governed by different factors, such as local regulations on the pet trade (Hulme 2007, 2009). Such factors fall outside the scope of this thesis. Therefore, I have excluded species considered introduced or invasive in the study area, following Howard et al., (2023). Additionally, seabirds, which spend most of their lives at sea have also been excluded. Their distribution is influenced by variables not examined in this thesis, such as change in the upwelling patterns or fish availability (Bakun et al. 2015, Dias et al. 2019). I included inland wetland species in this study, such as marsh terns (e.g., White-winged Tern - *Chlidonias leucopterus*) the factors driving their colonizations or extinctions (e.g., the extent of wetlands and climate change; (Soultan et al. 2022) are considered in this study. In the end, after I made the taxonomic corrections/conversions and excluded the exotic and marine species, I ended up with a total of 389 species/taxa. The list of all the bird species considered in this study is given in Appendix B.1.

2.2.4 Functional traits

In this chapter of my thesis, I utilized functional traits to investigate (i) how the functional composition and diversity of the breeding bird communities changed over the course of the study period (ii) how initial functional trait diversity of the

communities is related to their temporal functional and taxonomic stability (*iii*) to quantify their functional stability. I adopted the widely-accepted functional trait definition by Violle et al. (2007), which defines a functional trait as any morphological, physiological, or phenological characteristic of an organism that is measurable at the individual level, without reference to the environment or any other level of ecological organization. Throughout the study, I used the terms "trait" and "functional trait" interchangeably, so whenever the term "trait" appears in the text, it refers specifically to a functional trait.

Trait-based approaches are inherently sensitive to various methodological decisions, including the number and nature of traits chosen for the analyses (Petchey and Gaston 2006, Hordley et al. 2021). Despite its pivotal role in shaping the outcome of all the subsequent analyses, trait selection is sometimes poorly executed, potentially rendering the all trait-bases analyses obsolete or making it difficult to detect existing ecological relationships (Luck et al. 2012, Rosado et al. 2013). To avoid the common pitfalls in trait selection (see Lefcheck et al. (2015) for an overview), I followed several published studies as guidelines when selecting the traits for this study.

The trait selection process should ideally begin with identification of relevant environmental drivers and ecosystem processes (Luck et al. 2012, Rosado et al. 2013). Next, using specific knowledge about the focal taxa, the processes governing their responses to these environmental drivers should be determined (Petchey and Gaston 2006, Rosado et al. 2013). Once these processes are understood, connections between them and potential functional traits should be established to derive a set of traits relevant to the specific case (Luck et al. 2012, Rosado et al. 2013). At this stage, data availability should also be considered as an additional filter (Luck et al. 2012). Finally, the traits should be processed further to address issues like correlation to obtain the final trait list (Leps et al. 2006, Luck et al. 2012).

In the end, the selected traits should all be important for the functions, processes of interest, relevant in the context of ecological questions asked, applicable to the focal organism group, and accessible (Petchey and Gaston 2006, Luck et al. 2012). As for

the number of traits, there is no universal guideline that fits all cases and studies (Petchey and Gaston 2006). Eventually, the number of traits chosen will depend on the outcomes of the steps listed above and the subjective decisions taken by the people conducting the study. However, the researchers should prefer using multiple traits over a single trait whenever their questions or hypotheses are multi-faceted (Leps et al. 2006, Lefcheck et al. 2015). For instance, if there are multiple environmental drivers shaping a community, they may leave different “functional” signatures in trait composition of that community (Lefcheck et al. 2015). In such cases, using multiple traits can allow for a more complete functional representation of the community. However, many is not always better. The relevance of the traits is far more important than their quantity, as a few well-chosen, highly relevant traits can be better predictors of community responses or processes than many poorly chosen, ecologically irrelevant traits (Leps et al. 2006, Lefcheck et al. 2015). Furthermore, utilizing a high number of traits can also cause the diversity of functional traits to mirror taxonomic richness (Lefcheck et al. 2015), while also introducing a significant, yet unnecessary, computational complexity when calculating multi-dimensional trait diversity indices (Maire et al. 2015, Mouillot et al. 2021).

Earlier in this chapter of the thesis, I have already listed the potential drivers of community stability and laid out my hypotheses regarding the effect of each driver on community stability (section 2.1.3). Following the steps outlined in the previous paragraph, I came up with a list of candidate functional traits. Fortunately, birds are one of, if not, the best-studied vertebrate group, with numerous databases providing trait data for dozens of functional traits across thousands of species (Wilman et al. 2014a, Tobias et al. 2022). As a result, data availability was not a significant issue in my case.

I also adopted a response-effect trait framework approach (Violle et al. 2007b, Luck et al. 2012, Hordley et al. 2021), classifying the candidate traits as response and/or effect traits. Response traits are traits that moderate how species response to changes in their environment, whereas effect traits are the ones that determine the effect a

species has on ecosystem (Hordley et al. 2021). Functional traits related to multiple niche dimensions can sometimes qualify as both response and effect traits simultaneously (Elmqvist et al. 2003, Luck et al. 2012, Volaire et al. 2014, Hordley et al. 2021).

Since community stability is the primary focus of this chapter, and given that communities with high response diversity are expected to remain more stable thanks to the diverse set of ecological requirements and tolerances within the community (Luck et al. 2012, de Mazancourt et al. 2013c, Hordley et al. 2021), I selected traits primarily based on their role as response traits. Ultimately, I selected six traits for this study: body mass, relative brain mass, the Hand-Wing Index (HWI), breeding season diet, foraging stratum, and breeding habitat. Five of these traits qualified as both response and effect traits, while relative brain mass qualified only as a response trait.

The six selected traits are highly relevant to the ecological context of this study, and they collectively cover various dimensions of the Eltonian and Grinnellian niche of the breeding bird communities (Soberón 2007, Luck et al. 2012, Wilman et al. 2014a). Table 2.6 provides a list of these traits, including their levels, trait types (response, effect or both), variable types (continuous, binary, or fuzzy), the sources used for scoring, and their ecological significance. One of the traits used in this study, breeding habitat preference (see below), does not fully conform to the definition given in Violle et al. (2007), as it cannot be measured without reference to the surrounding environment. Nevertheless, I chose to retain this trait in my analyses owing to its strong influence on the responses of breeding birds to environmental changes, such as those related to climate and land cover (Luck et al. 2012, Chevalier et al. 2019), which are central to this study. Other than relative brain mass, the only morphological trait used in this chapter was body mass (Table 2.6). This is because other morphological traits are often highly correlated with body mass due to allometric relationships (Tobias et al. 2022). While I acknowledge that other morphological traits, such as body length and bill length, are highly relevant and influential traits (Luck et al. 2012, Özgencil et al. 2020), body mass remains as the

single most informative trait due to its correlation with many other traits. Therefore, I chose to retain body mass alone to simplify the analysis and reduce the number of trait dimensions, making trait-based calculations more manageable. Detailed information on how the traits were scored and processed is provided in sections from 2.2.4 to 2.2.6.

All trait-based analyses in this chapter follows the protocol for reproducible functional diversity analyses outlined by Palacio et al. (2022). This is to make sure I follow a standard reporting scheme, good practices for data processing and analyses, and generate a fully reproducible piece of scientific work. I have also used their web-based application called *stepFD*, which allows researchers conducting trait-bases analyses to check the requirements needed at each step of the analyses to make their study fully reproducible and create a reproducibility report. The application is available at <https://facuxpalacio.shinyapps.io/stepFD/> and the reproducibility report for this study is provided in Appendix B.2.

Table 2.6 Functional traits used in the chapter, their levels, trait types, variable types, sources used to score them, and their ecological relevance. Full citations of the references used in the table are included in the references section of the chapter. R: response, R&E: response and effect, C: continuous, B: binary, F: fuzzy.

<i>Trait</i>	<i>Levels</i>	<i>Ecological relevance</i>	<i>Trait type</i>	<i>Variable type</i>	<i>Sources</i>
Body mass	NA	Resource requirements, metabolic rate, thermoregulation, trophic level, biotic interactions, dispersal/movement ability, extinction vulnerability, contribution to ecosystem functions (e.g., seed dispersal, pest control, and nutrient transportation), longevity, home range size	R&E	C	Tobias et al. (2022)
Breeding habitat	Shrub Tundra Rocks Grassland Settlement Wetland Forest & woodland	Spatial niche partitioning, biotic interactions, response to environmental changes and disturbances (e.g., habitat loss), contribution to ecosystem functions (e.g., seed dispersal and nutrient deposition)	R&E	B	Storchová & Hořák (2018)
Breeding season diet	Invertebrates Vertebrates: terrestrial Vertebrates: fish Plants: fruit & nectar Plants: other & seeds	Trophic level, biotic interactions, resource requirements, contribution to ecosystem functions (e.g., nutrient recycling and nutrient deposition), response to environmental changes and disturbances (e.g., changes in vegetation structure and cover), spatial niche partitioning	R&E	F	Murphy et al. (2023)
Foraging stratum	Ground Understory Midhigh & canopy	Biotic interactions, resource requirements, spatial niche partitioning, response to environmental changes and disturbances (e.g., habitat loss), contribution to ecosystem functions (e.g., nutrient deposition)	R&E	F	Wilman et al. (2014)

Table 2.6 (continued)

Hand-Wing Index (HWI)	NA	Flight strength, flight efficiency, dispersal/movement ability, response to environmental changes and disturbances (e.g., fragmentation), contribution to ecosystem functions (e.g., seed dispersal and nutrient transportation), migratory behavior	R&E	C	Tobias et al. (2022)
Relative brain mass	NA	Capacity to adapt to novel environments, response to changes in environment and disturbances, behavioral flexibility	R&E	C	Galván & Møller (2011), Garamszegi et al. (2002), Iwaniuk (2004), Jiménez-Ortega et al. (2020), Minias & Podlaszczuk (2017), Sayol et al. (2020), Sol et al. (2010), Tsuboi et al. (2018)

2.2.5 Trait scoring, processing, and distributions

Table 2.6 presents the final processed forms of each trait used in this study. However, each selected trait underwent a thorough processing procedure before reaching their final forms. In this section, I will describe the scoring and processing steps, and present the distributions of each trait.

I used the AVONET database (Tobias et al. 2022) to score the body mass trait. AVONET uses Dunning (2007) as its main data source, while presenting updated body mass data for some of the species. Figure 2.8a shows the distribution of the raw body mass data for the 389 study taxa.

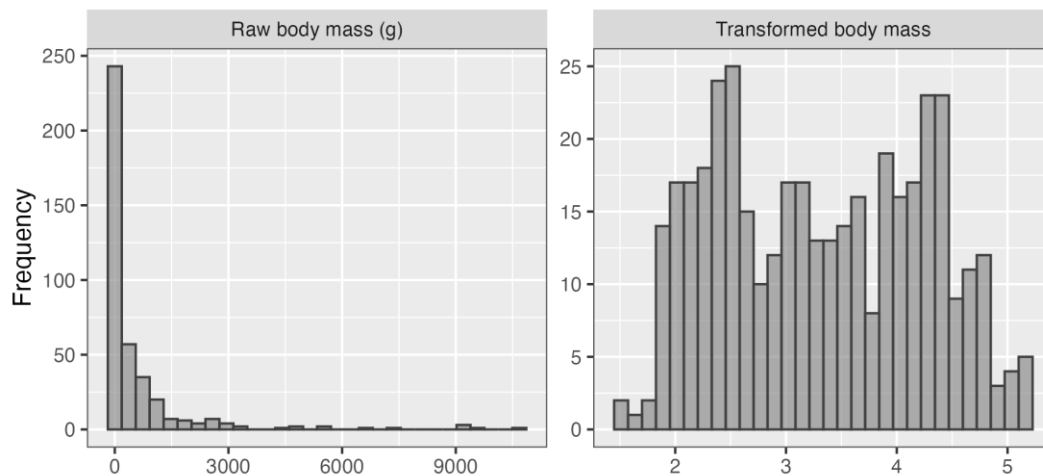


Figure 2.8 Distributions of raw body mass data (left) and its transformed version (right).

As shown in figure 2.8a, the distribution of the body mass trait was highly skewed, a common characteristic of size-related traits (Leps et al. 2006, Májeková et al. 2016, Götzenberger et al. 2020). In cases like this, data transformation is often recommended as a method to minimize the high effect of extreme values (Leps et al. 2006, Pavoine et al. 2009, Májeková et al. 2016). Although Gower distances, which standardizes data to account for differences in scale and range (Gower 1982, de Bello et al. 2013), will be used to calculate the pairwise distances (see section 2.2.6)

between the study taxa, this approach does not fully address the issue of the different distribution of dissimilarity across traits (de Bello et al. 2021a). Such differences in distribution can cause certain traits, such as categorical or highly skewed ones, to contribute disproportionately to overall dissimilarity simply because of their greater variance (Götzenberger et al. 2020, de Bello et al. 2021a). For instance, combining a quantitative trait with a relatively low variance and a near-normal distribution with another trait that has a relatively greater variance and a skewed distribution, the multi-trait dissimilarity is expected to be more correlated to the latter (de Bello et al. 2021a). This emphasizes the importance of carefully treating trait data before calculating functional diversity indices, as the distribution of traits can significantly impact the results (Pavoine et al. 2009, Májeková et al. 2016).

Since improvements in normality are expected to enhance the accuracy of functional diversity metrics (Májeková et al. 2016) and promote a more balanced contribution of individual traits to overall dissimilarity (Götzenberger et al. 2020), it is common practice to employ data transformation, such as log transformation, in the case of skewed trait data prior to distance calculations using Gower distances or even the gawdis method (Leps et al. 2006, Pavoine et al. 2009, Götzenberger et al. 2020, de Bello et al. 2021a). Both Gower distances and the gawdis method are described and discussed in section 2.2.6. Because of the reasons listed above, I decided to follow the suggestions of de Bello et al. (2021) and Götzenberger et al. (2020) and transformed the raw body mass prior to trait-based analyses. However, rather than simply log-transforming the body mass trait as commonly suggested (e.g., Leps et al., 2006), I opted for the Box-Cox transformation to automatically find the most efficient normalizing transformation (Legendre and Legendre 2012). For this purpose, I used the *boxcox* function from the *MASS* package (Venables and Ripley 2002). The optimal λ was -0.14, which I used to carry out the transformation. The distribution of the transformed data is shown in Figure 2.8b, where clearly demonstrates that the data now approximates a normal distribution better.

I used Storchová & Hořák (2018)'s Life-history characteristics of European birds database to score the breeding habitat trait. The database originally includes 15

habitat categories, two of which, savanna and marine, were outside the geographic scope of the current study and were therefore excluded. High dimensionality in functional trait data can be an extreme computational burden in trait-based analyses (Swenson 2014, Mouillot et al. 2021). Therefore, I aimed to reduce the number of traits included in the analyses and selected only the most relevant ones. In order to reduce the dimensionality of the remaining levels of the breeding habitat trait, I grouped some of the levels into broader levels. First, I merged deciduous forest, coniferous forest, and woodland (woodland: habitats with disperse vegetation, edge of forest, etc., with presence of full-grown trees) into a single category representing all forests and woodlands. While I acknowledge that these habitats have ecological differences, they also share some common ecological features such as the presence of trees. Since this study does involve ecological questions regarding different forest types or forest-woodland comparisons, I decided to merge these levels to obtain a broader level, which would be more in line with the broad ecological questions asked in this thesis. Similarly, I combined swamp, reeds, and freshwater levels to obtain the broader wetland habitat. Again, this approach is more in line with the aims of the study, which does not involve ecological questions regarding differences among swamp, reeds, and freshwater habitats. Ultimately, I ended up with seven habitat categories: shrub, tundra, rocks, grassland, settlement, wetland, and forest & woodland (Table 2.6).

Many bird species have seasonally varying diets (Cramp 1977, Murphy et al. 2023). However, nearly all of the avian functional trait databases provide singular diet data that do not account for this plasticity. Since diet is closely related to the responses of birds to environmental changes (Luck et al. 2012), utilizing accurate diet data becomes crucial for studies concerning a certain season of the year and involving species that have seasonally varying diets. This is because a failure to use diet-related information representative of the time of the year of concern may render the trait uninformative, which can in turn impair detection of existing ecological relationships (Lefcheck et al. 2015). To address this, I utilized the recently published SAviTraits 1.0 database (Murphy et al. 2023), which provides information on temporal variation

in dietary preferences of more than 10,000 bird species. This database adopts the same dietary categories described by the widely-used EltonTraits 1.0 database (Wilman et al. 2014b), but presents data on the proportional use of each dietary category for each month of the year. Since this study focuses on breeding bird communities, I used spring and summer months' averages for each category and named the trait "breeding season diet".

Some of the diet categories had highly unbalanced distributions, with only several species having non-zero values, such as the "vertebrate: unknown", "scavenger", and "plant: nectar" levels (Figure 2.9). Consequently, I merged these categories with the other categories to obtain broader dietary categories. This was not the only reason that I merged dietary categories as sometimes I did it solely to reduce dimensionality and because it made ecological sense. For instance, I merged the "vertebrate: ectotherms" and "vertebrate: endotherms" categories solely to reduce dimensionality prior to analyses. While I recognize the fact that ectotherms and endotherms are physiologically and ecologically distinct, thus dietary categories representing these may also have different ecological significance. Nonetheless, both of these categories represent animal prey and combining them together generated a broader category similar to carnivory, which is ecologically relevant, as birds consuming these animals share predatory behaviors and a carnivorous diet. One might suggest it would be better to remove some of these traits, but doing so would result in a loss of information and artificial trait omission can have a detrimental impact on functional diversity analyses (Zhu et al. 2017, Mouillot et al. 2021) as discussed in Chapter 1. Ultimately, I ended up with five dietary categories: "invertebrates", "vertebrates: terrestrial", "vertebrates: fish", "plants: fruits & nectar", "plants: other & seeds" (Table 2.6). Other than the "invertebrates" and "vertebrates: fish" categories, all the remaining categories were obtained by merging multiple categories. The "vertebrates: terrestrial" was obtained by combining the ectotherm, endotherm, and unknown categories, the "plants: fruit & nectar" category was obtained by combining the fruits and nectar categories, and the "plants: other & seeds" category was obtained by combining the others and seeds categories.

Distributions of the diet category scores, including those of the excluded categories (aerial and scavenger), for the study taxa is shown in Figure 2.9 (a-g).

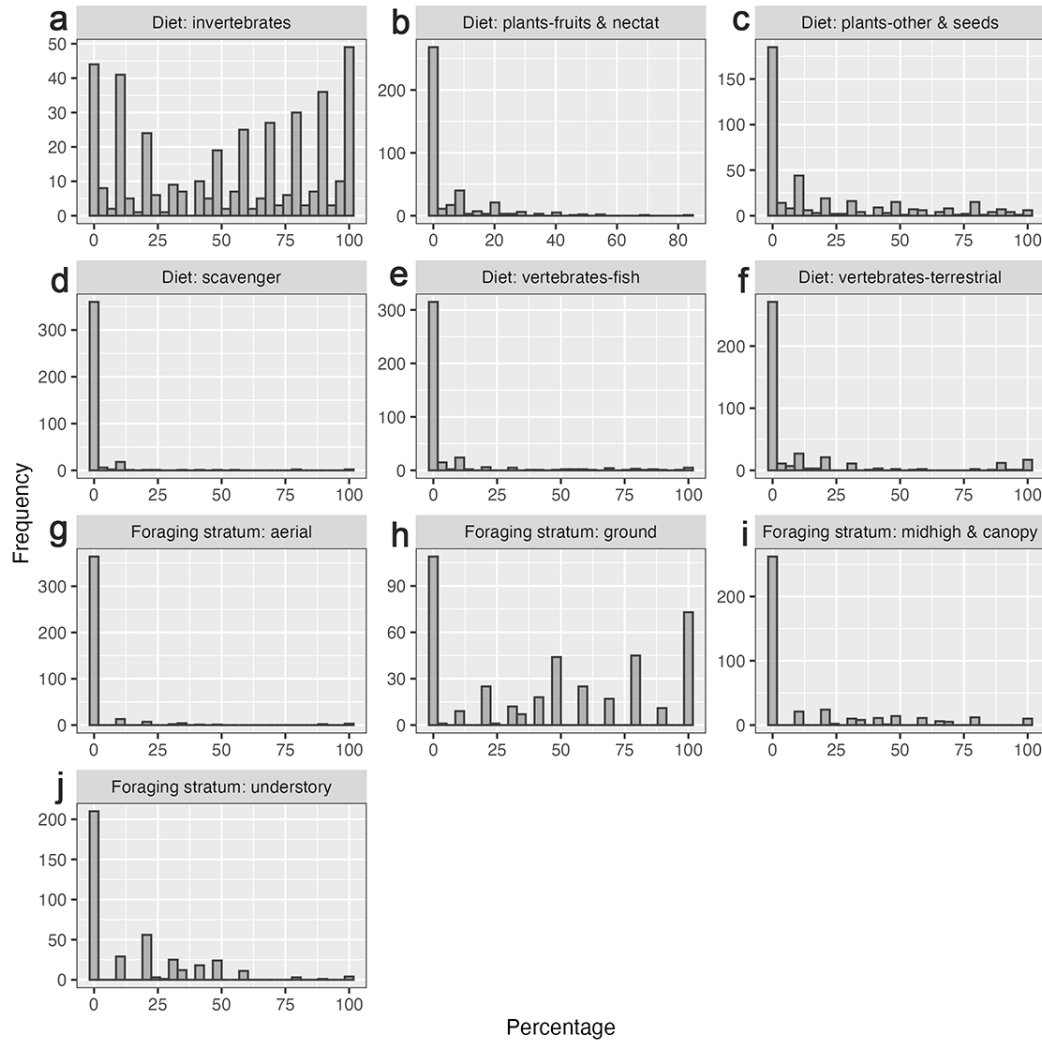


Figure 2.9 Distributions of the fuzzy traits used in the study (*a-f*: diet traits, *g-j*: foraging stratum traits) for the study taxa.

I used the Elton Traits 1.0 database to score the foraging stratum trait. The trait is scored as percentage of different strata that are used for foraging (Wilman et al. 2014a). As with the diet trait, I aimed to reduce the dimensionality prior to the functional diversity calculations. First, I combined the traits that describe the foraging at water surface and below the surface. This combined trait was strongly correlated with the "habitat: wetland" trait ($\rho: 0.84, p < 0.001^{***}$), which

represents the use of wetland habitats for breeding (see above). Including correlated traits in functional diversity calculations can artificially inflate their contribution to the metric, even when using ordination methods like principal coordinate analysis (PCoA; Lefcheck et al., 2015; Pavoine et al., 2009; Swenson, 2014). As a result, I removed this foraging stratum trait and retained the habitat trait instead, as it covers all wetland-breeding species, including those that do not forage on or in water, such as reed warblers.

Additionally, the aerial foraging stratum level, was found to be highly unbalanced with only 8% of the species using this stratum. Such unbalanced traits can have disproportionate contribution to functional diversity calculations as discussed earlier and should be removed (de Bello et al. 2021a), which is why I removed it from my dataset. In an attempt to further reduce the dimensionality of the data, I combined the canopy and midhigh (midhigh: mid to high levels in trees or high bushes- 2m upward- but below canopy; Wilman et al., 2014) strata into a single stratum. Once again, while I acknowledge that the vertical niche partitioning can be important for forest-dwelling birds (e.g., Naikatini et al., 2022), and levels of this trait capture this niche dimension effectively, the forests in the study area are not structurally as complex as tropical forests, where vertical stratification can play a significant role in species coexistence patterns (Naikatini et al., 2022; Thiel et al., 2021). Therefore, using coarser foraging stratum traits to represent vertical niche partitioning seems sufficient for this study. Moreover, combining these two levels still provides an ecologically meaningful trait representing foraging in parts of trees above 2 meters from the understory. Together with the understory stratum, which indicates foraging below 2m in understory in forests, forest edges, bushes or shrubs, these two vertical foraging strata capture an important portion of the vertical niche dimension. In the end, I retained three levels to the foraging stratum trait: ground, understory, and midhigh & canopy.

I scored the HWI trait using the AVONET database. This trait is related to wing aspect ratio and wing pointedness (Claramunt et al. 2011, Arango et al. 2022). Specifically, HWI represents wing elongation, with high HWI values indicating

more elongated wings and low values indicating less elongated wings (Arango et al. 2022). This trait is considered as a valid proxy for flight and dispersal ability in birds (Dawideit et al. 2009). The formula used to calculate HWI is provided below in formula 2.1.

$$HWI = 100 \left(\frac{WL - SL}{WL} \right)$$

Here, length of the closed wing (WL) is subtracted from distance from the carpal joint to the tip of the first secondary feather (SL) to obtain the distance between the tip of the first secondary feather and the tip of the longest primary feather, which is also known as Kipp's Distance (Pyle 1997, Claramunt et al. 2011). This value is then divided by the wing length. Including wing length in the denominator helps reduce or practically eliminate the allometric effect of body mass on this morphological trait. Figure 2.10 shows the relationship between HWI and transformed body mass values for the 389 taxa included in the study.

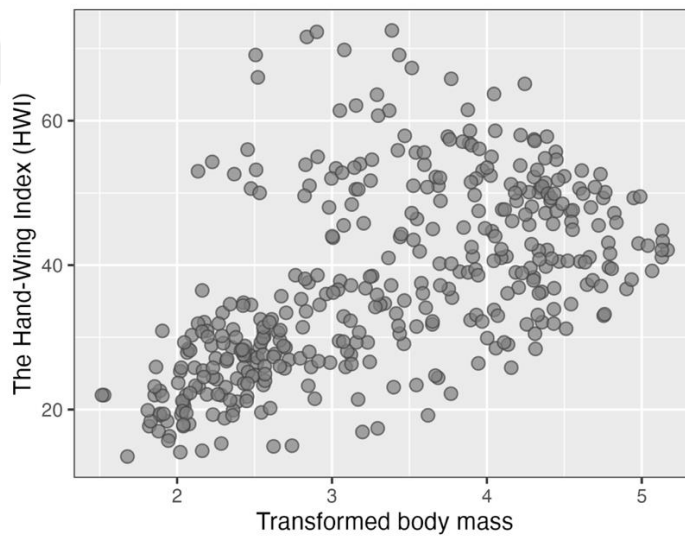


Figure 2.10 The Hand-Wing Index (HWI) and transformed body mass values of the 389 study taxa. Details on how the body mass trait was transformed is provided in the preceding paragraphs of the section.

I used the *cor* function from the base R (R Core Team 2024) to calculate correlations between trait pairs (see below for more details on correlation between the traits). The correlation between HWI and body mass variables was moderate, positive, and statistically significant ($\rho: 0.61, p < 0.001^{***}$). However, a visual inspection of the HWI vs. body mass plot did not suggest any clear linear relationship between the two traits (Figure 2.10). The correlation coefficient threshold I used in this study was 0.70, above which I considered traits to be strongly correlated and either removed or further processed one of them. This threshold is quite conservative considering that some of the studies set their correlation thresholds at 0.80 (e.g., Johnson et al., 2015). Given that the visual inspection of Figure 2.10 indicated no significant linear dependency and that the strength of the correlation was below the threshold, I retained HWI in the study due to its strong ecological relevance (see Table 2.1).

I used multiple sources to compile the raw brain mass data (see Table 2.6 for a full list of sources used to score this trait). Despite using all published databases that I had access to while scoring this trait, brain mass data was available for 81% of the study species, making brain mass the only trait with I missing data in this study.

Being a size-related trait, raw brain mass strongly and positively correlated with body mass ($\rho: 0.96, p\text{-value} < 0.001^{***}$), indicating that these two traits should not be used together in their raw forms in functional diversity calculations.

There are a few alternative methods used to remove the allometric effect of body mass on brain mass, and the most effective and commonly-used of these is the use of residuals from an ordinary least squares (OLS) linear model, where brain mass is regressed on body mass on a log-log scale (Sol et al. 2007, Sayol et al. 2016, Minias and Podlaszczuk 2017, Sayol et al. 2020a). This method produces a relative brain mass variable, where positive values indicate a brain mass that is larger than expected for a given body mass, and negative values indicate the opposite (Sol et al. 2007). Previous studies have shown that enhanced neural and cognitive capabilities are better represented by brain mass corrected for body mass rather than by raw brain mass (Sol et al. 2007, Sayol et al. 2016, Minias and Podlaszczuk 2017).

Based on this evidence, and to remove the allometric effect of body mass, I applied this approach to obtain a relative brain mass trait. For this purpose, I used the *glmmTMB* function from the *glmmTMB* package (Brooks et al. 2017) to fit a gamma generalized linear model (GLM; Zuur et al., 2009) with log link function regressing brain mass on body mass. The effect of log(body mass) was highly significant with an effect size estimate of 0.196 (SE: 0.004), and the model's R^2 value was 0.89. I then extracted the residuals from this model and used it as the relative brain mass trait in all of the trait-based approaches. The distribution of the relative brain mass trait is shown in Figure 2.11, and it is relatively normal. This is an advantage as the more normal the distribution of a trait is, the less sensitive the functional diversity indices became to missing trait information (Májeková et al. 2016). The total amount of missing trait data in this study was only around %1.

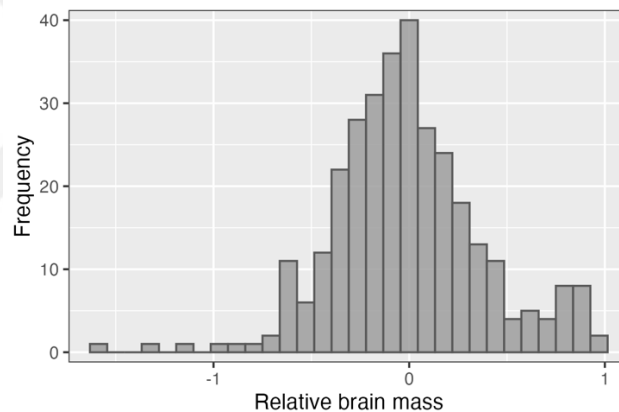


Figure 2.11 Distribution of the relative brain mass trait for the study taxa.

The correlation matrix, showing Spearman's rho for each pair of trait used in the study, is given in Figure 2.12. Since none of the traits were normally distributed, Spearman's rank correlation was used. As shown in the figure, none of the correlation coefficients was greater than 0.61 in absolute value, which lead me to conclude that the selected traits do not show substantial correlation, and it was appropriate to include them all in the subsequent analyses and calculations.

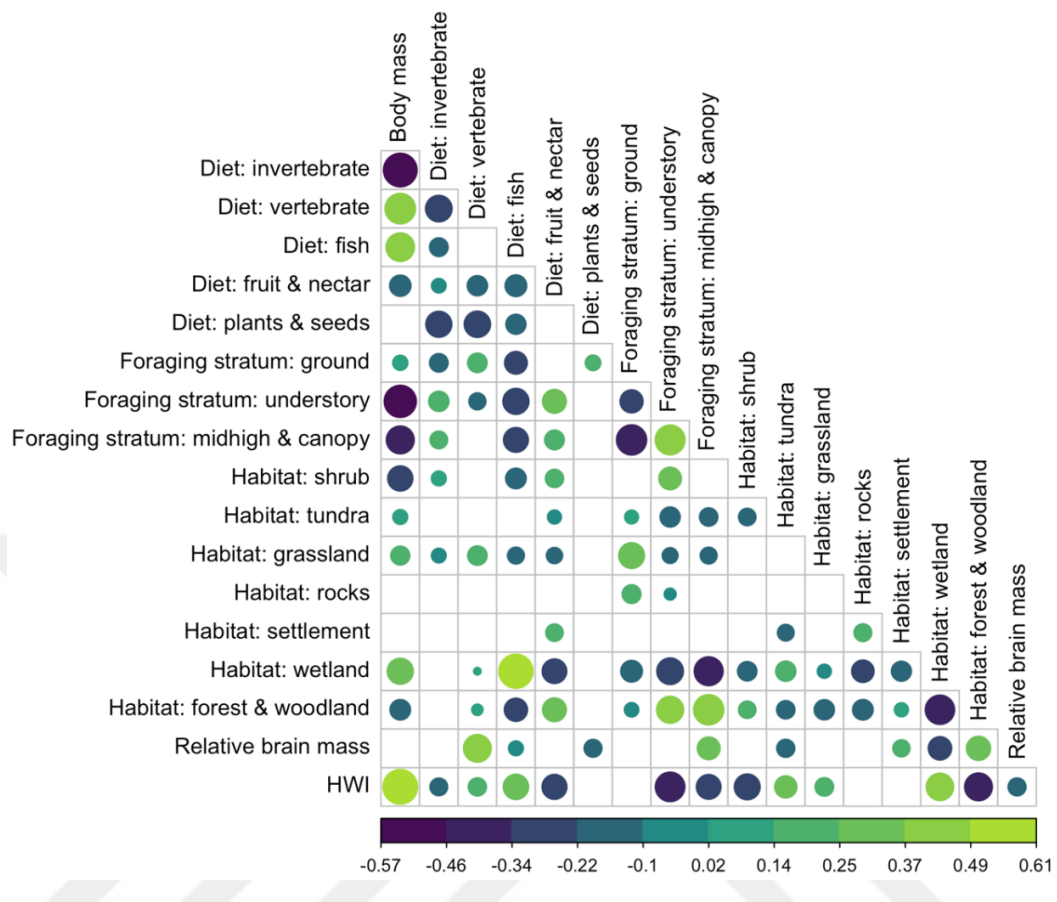


Figure 2.12 Correlation matrix displaying Spearman's rho (horizontal axis) for pairs of functional traits included in the study. Insignificant correlations ($\alpha = 0.05$) are not shown. The size of the circles indicates the absolute value or strength of the correlation.

2.2.6 Trait weighting and functional distance calculations

Calculation of many functional diversity metrics requires prior quantification of pairwise distances between the studied taxa in multi-dimensional “functional” space (Swenson 2014, Magneville et al. 2022). Gower distances (Gower 1966) are particularly useful for cases, where multiple types of traits such as fuzzy, binary, categorical, and continuous are considered (Pavoine et al. 2009, Legendre and Birks 2012, Swenson 2014). Moreover, by normalizing all variables to a [0,1] range, Gower distances ensure that no single trait type (e.g., one with a large range)

dominates the distance calculation (Gower 1966). The Gower distances also allow for differential weight assignment for individual traits during averaging trait dissimilarities into multi-trait dissimilarity (de Bello et al. 2021a). This means, a greater weight can be given to some traits to avoid them having a lower contribution to the overall dissimilarity or vice versa (Laliberté and Legendre 2010). Unfortunately, there is no objective way to assign these weights. One of the commonly-used strategies is to group traits into broader categories (e.g., morphological, phenological, habitat-use-related) and assign a weight of $\frac{1}{n}$ to each trait, where n is the number of traits in each group, so that each broader category gets the same weight. In case there are no broader categories, n simply can be the number of traits used in the study (e.g., Özgencil et al., 2020).

Recently, a new algorithm was published by de Bello et al. (2021), which is capable of calculating the optimal weight for each trait to ensure they all contribute nearly equally to the overall multi-trait dissimilarity. The algorithm comes within the *gawdis* function in the *gawdis* package (de Bello et al. 2021a). The *gawdis* function works by finding the weights that minimize the differences in the correlation between the dissimilarity of each trait and the multi-trait dissimilarity. Then, using these “optimal” weights, Gower distances are calculated. The function also allows for grouping of traits that may be correlated or traits providing similar biological or ecological information. When groups are defined, individual contributions of traits can be also be weighted to achieve comparable contributions within the groups. However, the group definition still remains a subjective decision in this approach. The function can also resolve fuzzy-coded traits, such as the diet and foraging stratum traits used in the study. Ultimately, the *gawdis* function offers a less subjective (compared to subjective weighting of the traits – see above) solution to produce multi-trait dissimilarity that has more uniform contributions of individual traits. Due to its advantages outlined above, I preferred the *gawdis* method over the subjective weighting to ensure comparable contribution of each individual trait and trait group to the overall multi-trait dissimilarity. To do this, I defined four trait groups: morphological, diet, foraging stratum, and breeding habitat preference. I

treated body mass, HWI, and relative brain mass as morphological traits and grouped them together following the suggestions provided in de Bello et al. (2021). The remaining three groups all were made up of levels or categories of single traits.

After finding the weights that allow comparable contributions by trait groups and traits within each group and calculating the pairwise “functional” distances for the study taxa using the *gawdis* function, I then ran a PCoA on the resultant pairwise distance matrix. PCoA is an ordination method suitable for mixed types of variables, just as Gower distances, which is used to visualize the similarity (or dissimilarity) of data points in a lower-dimensional space (Swenson 2014). PCoA using the non-Euclidean Gower distance matrix eventually leads to PC axes with negative eigenvalues. Gower distances may generate negative eigenvalues, indicating the non-Euclidean nature of the pairwise distance matrix (Gower 1982, Legendre and Birks 2012). There are various corrections that can be applied to these distance matrices to transform them into Euclidean distance matrices (Laliberté et al. 2014b, Magneville et al. 2022). Unfortunately, all of these corrections change the nature and distribution of the functional pairwise distances (see article 2 in the mFD package’s vignette for a thorough discussion), reducing the representativeness (Magneville et al. 2022). Therefore, I did not apply any corrections to while conducting PCoA on the distance matrix calculated using the *gawdis* method following the suggestions of Magneville et al. (2022).

2.2.7 Dimensionality reduction

Previous studies have pointed out that the number of PCoA axes used significantly influences the patterns of functional diversity metrics calculated (Villéger et al. 2011, Maire et al. 2015) because the new multi-dimensional space having lower number of dimensions achieved after the dimensionality reduction is not a perfect representation of the initial multi-dimensional space (Maire et al. 2015, Mouillot et al. 2021, Magneville et al. 2022). Reducing the number of dimensions is a common practice in trait-based analyses as using a high number of dimensions may not be

necessary in the first place because of collinearity of the traits and because it increases the computational difficulty of calculating indices (Baselga and Orme 2012, Swenson 2014, Maire et al. 2015, Mouillot et al. 2021).

Several measures have been proposed to measure the representative quality of the reduced multi-dimensional space (Mérigot et al. 2010, Swenson 2014, Maire et al. 2015). Here, I used three recently-developed measures, the mean absolute deviation (mad; Magneville et al., 2022) and the two area under the curve (AUC) methods (Mouillot et al. 2021), as well as the more traditional percent variation explained (Legendre and Legendre 2012) to carry out and assess the quality of dimensionality reduction. The mad metric measures the mean absolute deviation in pairwise functional distances from the original functional distances (Magneville et al. 2022). According to this index, the best space is the one with lowest mad value, indicating the lowest amount of deviation from the initial pairwise distances. The AUC method suggested by Mouillot et al. (2021) is based on a co-ranking matrix comparing the ranking of the functional pairwise distances between the reduced and unreduced spaces. The AUC values range between 0 and 1, with 1 representing the most optimal case where the ranks of pairwise distances are perfectly preserved during the dimensionality reduction. As a rule of thumb, AUC values above 0.80 are considered excellent, 0.70 are considered good or acceptable, whereas values below 0.50 are considered poor representations of the initial space (Mouillot et al. 2021). The first AUC method I used to assess the quality of dimensionality reductions in my thesis was the AUC value itself. The second AUC method I used to assess the quality of the dimensionality reduction is suggested by Mouillot et al. (2021) too, and it is based on the fact that increasing the number of dimensions bring diminishing AUC returns after a certain threshold. This second method is based on surpassing the AUC elbow inflection point which corresponds to the number of ordination axes beyond which the “cost”, which is defined as number of dimensions, exceeds the “benefit”, which is defined as the increase in AUC with each added dimensions (Mouillot et al. 2021). The first AUC method described here, remains the more subjective method because it involves an arbitrary threshold. The elbow inflection point, on the other hand, is a

more parsimonious and objective approach, yet it is not as standardized as the 0.70 threshold, hindering its ability to be used across different datasets for comparisons. I used the *mFD* (Magneville et al. 2022), *dimRed*, and *coRanking* (Kraemer et al. 2018) packages to calculate the mad and AUC values for different numbers of dimensions. The percent variation explained was determined using the output from the *pcoa* function in the *ape* package (Paradis and Schliep 2019) to calculate the percent variation explained.

Figure 2.13 shows the mad values for dimensionality reductions across the first 10 PCoA dimensions.

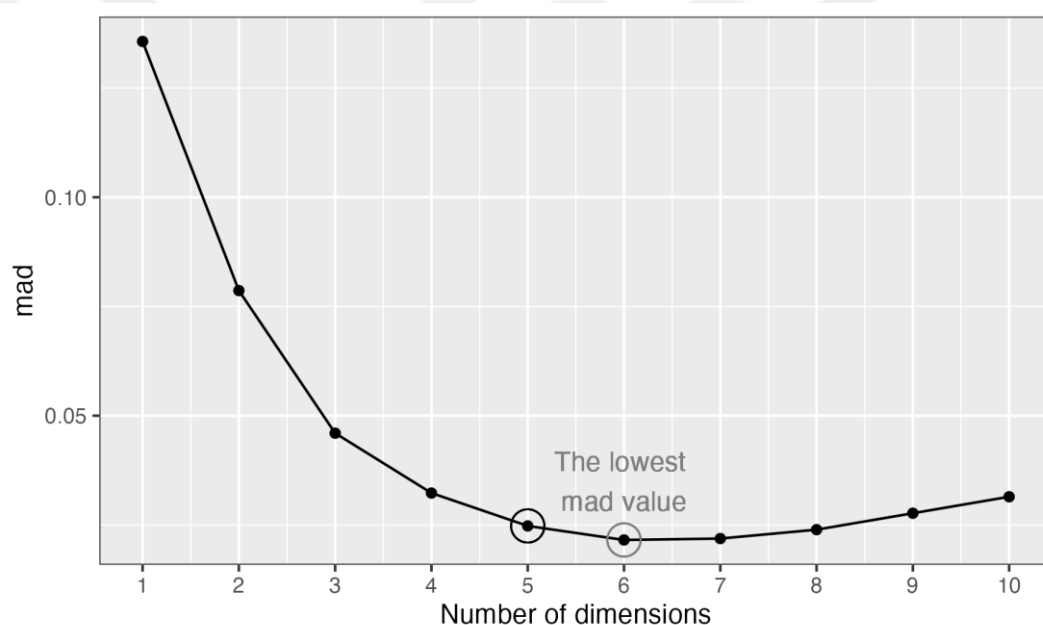
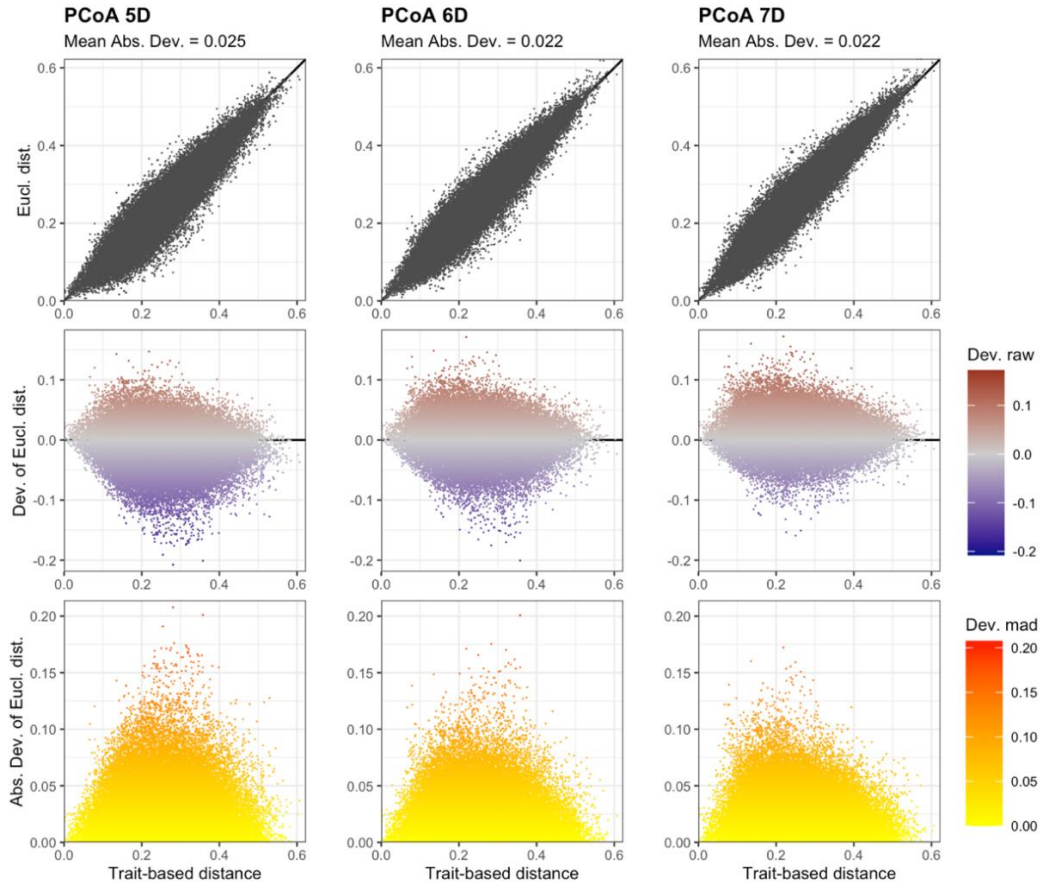


Figure 2.13 The mean absolute deviation (mad) metric values across the first 10 PCoA axes. The black circle marks the mad value for the chosen dimensionality reduction (i.e., the first five dimensions – see below), while the grey circle marks the dimension with the lowest mad value.

In my analyses, the lowest mad value was obtained when the first six PCoA dimensions were used in dimensionality reduction. The 5D space yielded mad values nearly as low as the 6D space. Figure 2.14 shows the output of the *quality.fspaces.plot* function, which presents the quality of the first five, six, and

seven dimensions using the mad metric, which I generated for further quality assessment using the mad metric.



Made with mfd

Figure 2.14 Quality assessment plots for the first five (left column), six (middle column), and seven (right column) PCoA axes with the mean absolute deviation (mad) metric. The upper row depicts the relationship between the pairwise distances in the original (y-axis) and reduced (x-axis) space. The middle row shows the raw deviations from the original pairwise distances across distances, and the lower row presents absolute deviations from the original Euclidean distances, both plotted across distances in the reduced space.

Figure 2.15 shows the results of the AUC-based quality assessment for dimensionality reduction across the first 10 PCoA axes.

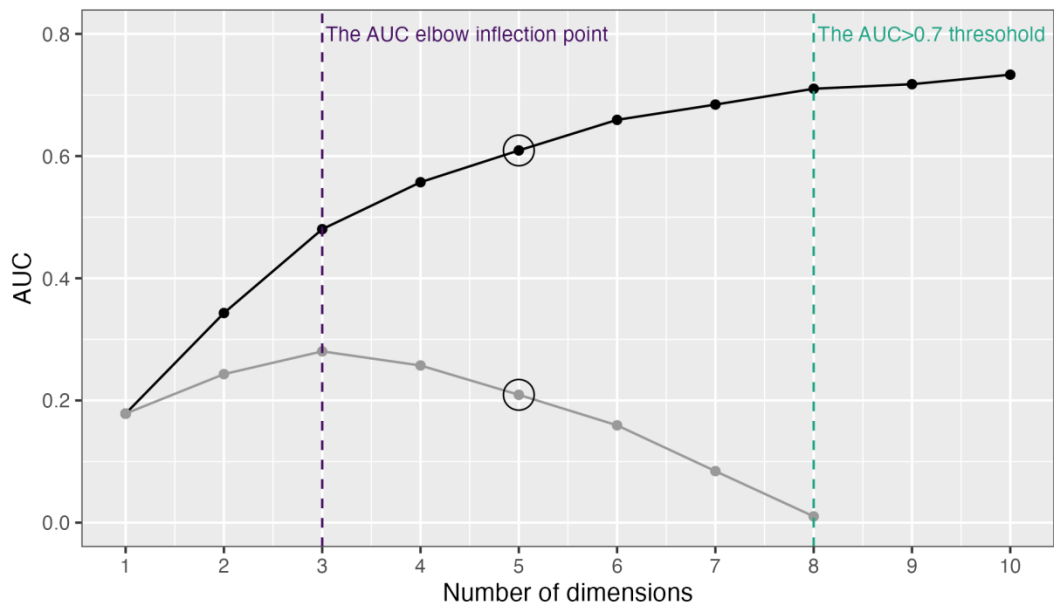


Figure 2.15 AUC (area under the curve) values (black line with dots, where dots indicate data points) and net AUC benefit (grey line with dots, where dots indicate data points) for dimensionality reduction scenarios using different numbers of PCoA axes. The black circles highlight the AUC (upper) and AUC benefit (lower) values for the chosen dimensionality reduction (i.e., the first five dimensions – see below). The purple dashed line (left) marks the AUC elbow inflection point, while the turquoise dashed line (right) marks the AUC > 0.70 threshold.

As shown in the figure, the AUC elbow inflection point occurs at the third dimension, indicating that the maximum gain in AUC benefit is achieved with three dimensions, beyond which there is diminishing returns in AUC. The arbitrary AUC > 0.70 threshold, on the other hand, is exceeded if the first eight PCoA axes are used.

The Percentage of variation explained by the use of first five PCoA dimensions is provided in Figure 2.16.

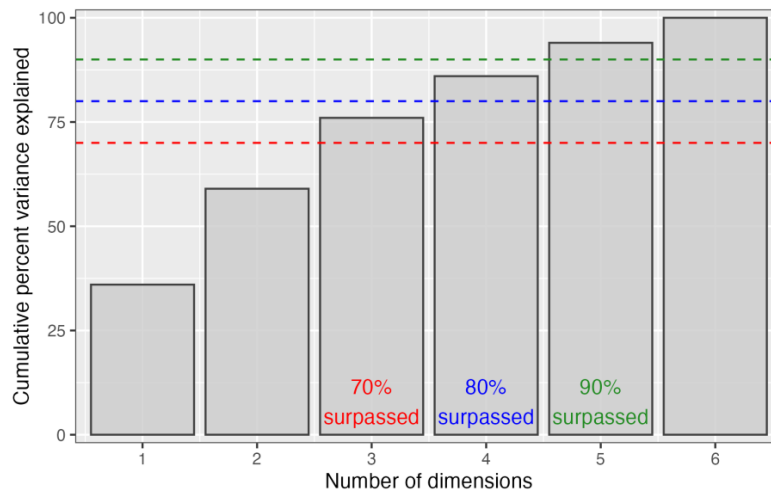


Figure 2.16 Percent variation explained by using up to give PCoA axes. The red dashed line (lower) represents the 70% threshold, the blue dashed line (middle) represents the 80% threshold, and the green dashed line (upper) represents the 90% threshold.

Figure 2.16 shows that the first five PCoA axes account for 94% of the variation in the original trait space.

After reviewing quality assessment results using AUC-based methods (Mouillot et al. 2021), the mad method (Magneville et al. 2022), and percent variation explained (Legendre and Legendre 2012), and keeping in mind that functional beta diversity calculations gets computationally very difficult beyond four or five dimensions (Maxime Logez, *pers. comm.*), I decided to use the first five PCoA axes for my trait-based analyses. With the first five PCoA axes, I achieved close-to-optimal mad values, with only a 15% higher mean absolute deviation (5D: 0.025 mad, 6D: 0.022 mad) compared to the optimal 6D space (Figure 2.13 and 2.14). The AUC score for the 5D space is 0.61, which is below the 0.70 threshold, but well above the AUC elbow inflection point (Figure 2.15). Finally, the 5D space chosen for this study explains 94% of the total variation in the original trait space (Figure 2.16), which is an impressive level of representation.

Some functional diversity metrics calculated, such as functional richness and functional dispersion (see below), require that species richness (S) is higher than the number of traits or trait dimensions included, the $S > t$ requirement (Mason et al. 2005b, Swenson 2014). Since the lowest species richness in the EBBA1 and EBBA2 datasets is 18, all squares met this requirement, and I did not have to exclude any square from analyses because of this requirement.

Dimensionality reduction and its assessment are further discussed in Appendix B.4.

2.2.8 Community stability

The community data used in this study were the two continental-scale breeding bird atlases conducted in Europe (see section 2.2.2). Since data were available from only two points in time, I could focus only on the resistance or compositional turnover components of stability, as studying variability or dynamic stability would require of data from more than two time points or prior knowledge of equilibrium states for community properties of interest, neither of which were available in this case (Donohue et al. 2013, McCallum 2015).

Since dataset consisted of presence/absence data, I quantified temporal taxonomic stability as compositional stability over time. To do this, I measured temporal beta diversity (Magurran 2013, Baselga et al. 2015). I preferred not to conduct any hypotheses testing with the turnover and nestedness components (Baselga 2010), as none of my research questions or hypotheses specifically focused on these individual components. I used total beta diversity (i.e., total dissimilarity) as a measure of taxonomic stability, where stability was calculated as $1 - \text{total temporal taxonomic beta diversity}$. However, I still calculated the turnover and nestedness components of taxonomic and functional beta diversity to gain insight into the nature of changes the communities experienced over the study period.

Here, I measured total beta diversity using Sørensen's dissimilarity index (Sørensen 1948, Magurran and McGill 2011). This index is a widely-used and effective

incidence-based dissimilarity metric, similar to the Jaccard's dissimilarity index (Magurran and McGill 2011, Hao et al. 2019). The main difference between the two is that while Jaccard's index compares the number of shared species to the cumulative number of species across the communities, Sørensen index compares number of shared species to the mean number of species in the communities (Sørensen 1948, Hao et al. 2019). This effectively makes Sørensen's index an overlap measure. Formula 2.2 gives the formula used to calculate Sørensen's dissimilarity (Sørensen 1948, Magurran and McGill 2011).

$$\frac{B + C}{2A + B + C} \quad (2.2)$$

In this formula, number of shared species is represented by A, while the numbers of unique species in each community are represented by B and C. As can be seen from the formula, when both communities have equal species richness, Sørensen's index simply reflects the proportion of species. I utilized the *beta.pair* function from the *betapart* package (Baselga and Orme 2012) to calculate pairwise total beta diversity between the “before” (during EBBA1) and “after” (during EBBA2) states of each community.

Recognizing the multi-dimensional nature of functional properties of breeding bird communities, I employed a multi-dimensional hypervolume approach and quantified multi-dimensional functional dissimilarity between “before” and “after” states of the study communities (Lengyel and Botta-Dukát 2023). This is unlike most of the studies, which primarily focused on a single niche dimension (see Introduction). Particularly, I quantified multi-dimensional functional dissimilarity for each study community as temporal functional beta diversity (Villéger et al. 2011). As with temporal taxonomic diversity, I used the incidence-based Sørensen's index to quantify temporal functional beta diversity (Magurran and McGill 2011). This approach has previously been applied to assess functional stability of bird communities (Oliveira and dos Anjos 2022). To ensure consistency, I used the same five PCoA axes derived from the dimensionality reduction wstep (section 2.2.7) to

calculate functional beta diversity. This ensured full compatibility between alpha (section 2.2.9) and beta functional diversity calculations in this chapter. I utilized the *functional.betapart.core.pairwise* and *functional.beta.pairwise* functions from the betapart package to calculate total temporal functional beta diversity and its components for each community. Here, as with taxonomic stability calculation, functional stability was defined as the inverse of functional dissimilarity or $1 - \text{total temporal functional diversity}$. The code used for calculating taxonomic and functional stability is available in the GitHub repository associated with this thesis.

2.2.9 Explanatory variables

In this section, I introduce the explanatory variables included in the analyses and provide information on their relevance, calculation, and sources I used to obtain data.

2.2.9.1 Intrinsic factors: Alpha taxonomic and functional diversity

Using multiple metrics to quantify functional diversity of communities is advantageous for multiple reasons; hence, I used multiple metrics to quantify functional diversity in my thesis. Firstly, functional diversity metrics are designed to capture different aspects and dimensions of functional diversity (Mason et al. 2005b, Mouchet et al. 2010). Some functional diversity metrics are designed to measure the amount of trait space occupied by a community, while some other metrics measure the distribution of species within this space, both of which are highly relevant in the context of community responses to change and stability (Villéger et al. 2008a, Moullot et al. 2013). Secondly, using multiple metrics can help better identify redundancy in ecological roles, which is directly linked with community stability and buffering capacity against environmental fluctuations (Petchey and Gaston 2002). Certain combinations of observations in different diversity metrics, e.g., low values of one metric combined with high values of another metric, might suggest

redundancy or complementarity among species, both of which are highly relevant to the ecological questions asked in my thesis (Petchey and Gaston 2006).

Below, I define the taxonomic and functional diversity metrics I chose for my study to quantify alpha-level or square-level diversity, provide visual representations for some of them, present the tools I used to calculate them, and postulate my hypotheses on the effect of these metrics or their combinations on community stability. Since the data I am using in this thesis is presence/absence data, I only calculated and used incidence-based versions of the metrics given below in my analyses.

Firstly, I used species richness to quantify the taxonomic diversity of the communities. Species richness is probably the most widely-used and intuitive taxonomic diversity metric used in ecological studies (Magurran and McGill 2011). In this study, it was the only taxonomic metric I could use, as other commonly used indices, such as the Shannon's indices, require abundance data, which was not available (Shannon 1948, Magurran and McGill 2011).

Functional richness (FRic; Mason et al., 2005; Villéger et al., 2008) measures the amount of trait space occupied by a community. For a multi-trait scenario, FRic is measured as the volume of the convex hull that includes all the species in the community (Figure 2.17a; Cornwell et al., 2006; Villéger et al., 2008). It is usually interpreted as an indicator for potentially used or unused trait or niche space (Mason et al. 2005b). FRic is expected to be somewhat positively correlated with species richness, though the exact relationship between FRic and richness can take many different forms (Schleuter et al. 2010). However, FRic has no a priori defined relationship with other functional diversity metrics (Mouchet et al. 2010). FRic is an incidence-based metric and cannot be weighted using abundances (Cornwell et al. 2006, Villéger et al. 2008a). I used the *fd_fric* function from the *fundiversity* package (Grenié and Gruson 2023) to calculate FRic for the communities in EBBA1 and EBBA2 datasets.

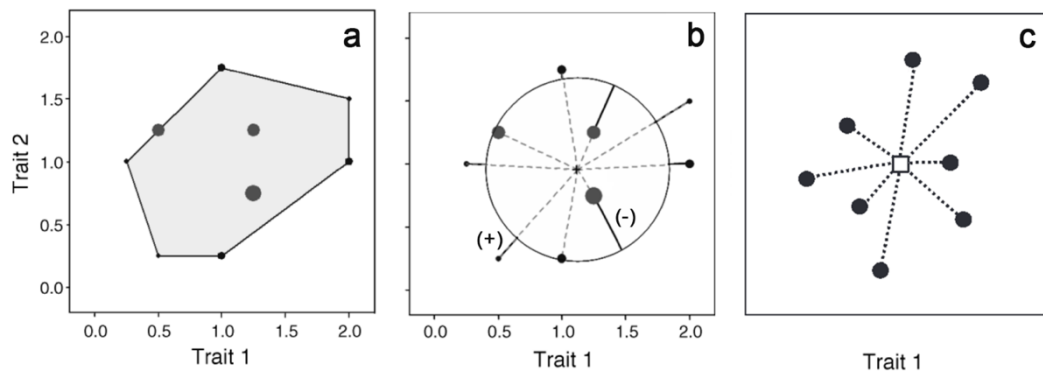


Figure 2.17 Visual representations of (a) functional richness, (b) functional divergence, and (c) functional dispersion. The dots indicate species positions in the trait spaces. Modified from Laliberté & Legendre (2010) and Villéger et al. (2008).

Functional evenness (FEve; Villéger et al., 2008) measures how evenly the abundances or biomass is distributed within the trait space occupied. FEve can be maximized when the distances between nearest neighbors are equal and when the abundances are equal (Mouillot et al. 2005, Schleuter et al. 2010). Then, incidence-based version of FEve simply measures how equal the distances between the nearest neighbors are. The metric is generally used to understand how effectively the entire range of resources are used by a community (Schleuter et al. 2010). A low FEve indicates that there are separate clusters of species in the trait space, leading to under-utilization of in some parts of the occupied trait space (Mason et al. 2005b). FEve is independent of species richness, FRic, and divergence or dispersion-based metrics (see below). I used the *fd_feve* function from the *fundiversity* package to quantify the FEve metric.

Functional divergence (FDiv; Villéger et al., 2008) relates to how abundance is distributed within the occupied trait space, and it is higher when the most abundant species have extreme trait values and it is low when the most abundant species have average trait values, positioning them close to the centroid of the community in multi-dimensional trait space (Figure 2.17b; Villéger et al., 2008). FDiv can include abundances in its calculation. High values of FDiv may indicate a high degree of niche differentiation and thus more efficient resource use and increased ecosystem

function (Mason et al. 2005b). This index is independent to FRic and FEve (Mouillot et al. 2005, Mouchet et al. 2010). I utilized the *fd_fdiv* function from the *fundiversity* package to calculate FDiv values for the study communities.

Functional dispersion (FDis; Laliberté & Legendre, 2010) index quantifies the dispersion of trait values of species in a community: it is simply the mean distance of species to the centroid of the whole community in trait space (Figure 2.17c). Abundances of individual species can be incorporated in this metric by weighting the distances to the centroid by abundances and by computing a weighted centroid (Laliberté and Legendre 2010). FDis may be strongly correlated with another similar dispersion metric, Rao's Q (Botta-Dukát 2005), but it does not have any a priori defined relationship with species richness and other functional diversity metrics (Laliberté and Legendre 2010). The *fd_fdis* function from the *fundiversity* package was used to quantify this metric.

I used two different functional redundancy metrics in my thesis. The first one is the R index from Ricotta et al. (2016). The whole idea behind this metric is the notion that species with similar trait values are likely to have similar ecological responses and roles, making the community functionally redundant (Mouillot et al. 2013). Formula to calculate the community-level R is given below in formula 2.3.

$$R = 1 - \frac{Q}{D} \quad (2.3)$$

Q in this formula represents Rao's Q, which is simply the mean dissimilarity of an individual (in the abundance-based version of the index) or a species (in the incidence-based version of the index) from the whole assemblage (Botta-Dukát 2005). D here indicates the well-established Simpson's D which gives the probability of two randomly chosen individuals from the community to belong to the same species (Magurran and McGill 2011). This means that a community with many species each having equal abundances would have a high Simpson's D value, indicating low diversity. It can be seen from the formula 2.3 that R can be maximized if Rao's Q is low, indicating clustering of species and biomass in trait space, and

when D is low, indicating dominance of a few species in the community or a less even community structure, in the incidence-based version of the index (Ricotta et al. 2016). Values of R range between 0 and 1.

The second functional redundancy metric used in this study is R* or Rstar defined in Pavoine & Ricotta (2019). R* is an alternative measure of redundancy that normalizes redundancy with respect community diversity. Since R* involves normalization in its calculation, it yields a measure that is potentially more comparable across communities with different diversity levels. The formula for R* is provided in formula 2.4.

$$R^* = \frac{Q - D}{1 - Q} \quad (2.4)$$

Here, the normalization with 1–Q allows R* to be more comparable across communities because it adjusts for differences in both species richness and trait distribution. The value of R* ranges between 0 and 1, and it is maximized when both Q and D approach zero, just as R. Both R and R* can incorporate abundance data as long as Q and D are calculated using abundance data. I used the *uniqueness* function from the *adiv* package (Pavoine 2020) to calculate R and R* redundancy indices.

Community-level functional originality (FOri; Magneville et al., 2022; Mouillot et al., 2013) quantifies the functional distance of each species in a community to its nearest species in the global species pool, averaged across all species in a community. The index can incorporate species abundances of the species by weighting the distances using abundances. FOri increases with the level of isolation of species in the community within the functional or trait space (Mouillot et al. 2013). I used the *alpha.fd.multidim* function from the *mFD* package (Magneville et al. 2022) to calculate FOri.

Functional specialization (FSpe) measures the distance of each species in a community to the centroid of the global species pool, calculated across all species in a community (Bellwood et al. 2005, Mouillot et al. 2013). FSpe also has an abundance-weighted version, which weights distances to the centroid by species

abundances (Mouillot et al. 2013). Having more species that are located far away from the centroid of the global species pool increases FSpe, while having more species with average or typical trait values, with respect to all species present in the global species pool, decreases FSpe. I calculated community-level FSpe for each EBBA1 square using the *alpha.fd.multidim* function from the *mFD* package.

I quantified the functional mean pairwise distance (FMPD) and functional mean nearest neighbor distance (FNND) for the study squares (Weiher et al. 1998). FMPD is defined as the mean distance between all pairs of species, while FNND represents the mean distance to the nearest neighbor calculated across all species within the community (Weiher et al. 1998, Magneville et al. 2022). Both metrics can be weighted by species abundances, incorporating abundance into the distance calculations. Although, I did not directly include these two metrics in my analyses, I used them alongside other metrics to formulate my hypotheses on the effect of functional structure or diversity of community on community stability (see section 2.1.3.2). I utilized the *alpha.fd.multidim* function from the *mFD* package to quantify FMPD and FNND metrics.

2.2.9.2 Extrinsic factors

I analyzed 19 different extrinsic variables to identify the ones that influence taxonomic and/or functional stability of breeding bird communities in Europe. In the following sections, I have described these variables and data sources I used.

2.2.9.2.1 Time gap between consecutive surveys and country identity

Time gap between two consecutive surveys is an important determinant of community similarity and stability, with communities observed over shorter intervals exhibiting higher similarity in species composition and thus functional composition (Lehman et al. 2000, Ives et al. 2003). Consequently, it is highly intuitive to suggest that communities sampled over shorter time intervals would

appear more stable or similar simply because various aspects of a community at time $t+x$ would depend on its state at time t , where x is a positive value (Legendre and Gauthier 2014). Therefore, I decided to include time gap between the consecutive survey dates for a square as a covariate in my analyses.

Survey dates for the squares were only available at country scale for EBBA1 and EBBA2, and the survey dates for countries were given as ranges in years (Table 2.1 and 2.3; Hagemerijer & Blair, 1997; Keller et al., 2020). Given the unavailability of exact survey years for each square, I used the mid-point of the survey year ranges for each country for all squares in that country for both EBBA1 and EBBA2. For squares spanning more than one country, I based the country assignment on the land surface area shares, assigning the country with the highest share.

There have been changes in political boundaries in my study area, such as splitting of Yugoslavia into multiple countries (Hagemerijer and Blair 1997). For squares in this area, I used the shared survey dates from the EBBA1 but used the new individual national survey dates from EBBA2. In the end, for example, for a country with an EBBA1 survey date range of 1985-1988 (mid-point: 1986.5) and an EBBA2 survey date range of 2013-2016 (mid-point: 2014.5), the time gap between the surveys would be $2014.5 - 1986.5 = 28$ years. When calculating the mid-point for the EBBA2 survey date ranges, I also took into account the percentages (i.e., percentages of total data collected) provided in Table 2.3 in section 2.2.2.2. In the end, the mean length of the time gap between the two surveys for the study squares was 29.1 years with a minimum of 21.0 and a maximum of 43.0 years.

Since countries in the study region differ in their nature conservation efforts, legislations regarding protection of wildlife (Jones-Walters and Čivić 2013), and the methods of atlas data collection (Hagemerijer and Blair 1997, Keller et al. 2020), country identity has the potential to be an influential explanatory variable in my analyses. Therefore, I included country identity in the models as a random effect (Zuur et al. 2009b) to account for any potential country effect.

2.2.9.2.2 Mean elevation

Mean elevation of an area can potentially be an influential factor in determining the stability of the communities it hosts (Brooks et al. 2002, Körner 2004, La Sorte and Jetz 2010). To test the effect of mean elevation on community stability, I downloaded GTOPO30: Global 30 Arc-Second Digital Elevation Model (USGS 1996), which offers a fine 1-km spatial resolution and processed it in Google Earth Engine (Gorelick et al. 2017) to calculate elevational variance for each study square.

2.2.9.2.3 Land surface area

Land surface area can play an important role in community stability (MacArthur and Wilson 1967, Simberloff and Abele 1976, Whittaker and Fernandez-Palacios 2007). The 50 km x 50 km UTM grid squares used in this study do not always have the same shape and area due to inherent issues with projection systems like the UTM system (Hager, 1988). Furthermore, grid squares with coastal locations usually have smaller land areas (the study focuses on landbirds and inland wetland birds – see section 2.2.3), compared to the continental ones. For these reasons, the squares included in this study can have different land areas. Therefore, I included it as a covariate in my thesis to test its potential impact on the stability of breeding bird communities in Europe. Data for land surface area in each study square was obtained by processing GTOPO30: Global 30 Arc-Second Digital Elevation Model (USGS 1996) on Google Earth Engine (Gorelick et al. 2017).

2.2.9.2.4 Protected area coverage

Wildlife inside protected areas may be protected better from human actions (Joppa and Pfaff 2010) and may remain more stable over time. For this reason, I decided to include the proportional coverage of protected area in study squares as covariates in my community stability analyses. To do that, I downloaded the World Database on

Protected Areas (WDPA) from <https://www.protectedplanet.net> in high-resolution vector format, and processed it in R (R Core Team 2024) using the *sf* package (Pebesma 2018). This dataset uses the International Union for Conservation of Nature's (IUCN) protected area categories (Dudley et al. 2010), which are strict nature reserves (category *Ia*), wilderness areas (category *Ib*), national parks (category *II*), natural monuments or features (category *III*), habitat/species management areas (category *IV*), protected landscapes (category *V*), and protected areas with sustainable use of natural resources (category *VI*; Dudley et al., 2010). The detailed descriptions of each of these categories, along with their eligibility criteria, are provided in Dudley et al. (2010) and Stolton et al. (2013). After cropping the protected areas layer using the boundaries of my study area in R by using the *sf* package, I calculated the total area of each category of protected area (Figure 2.18).

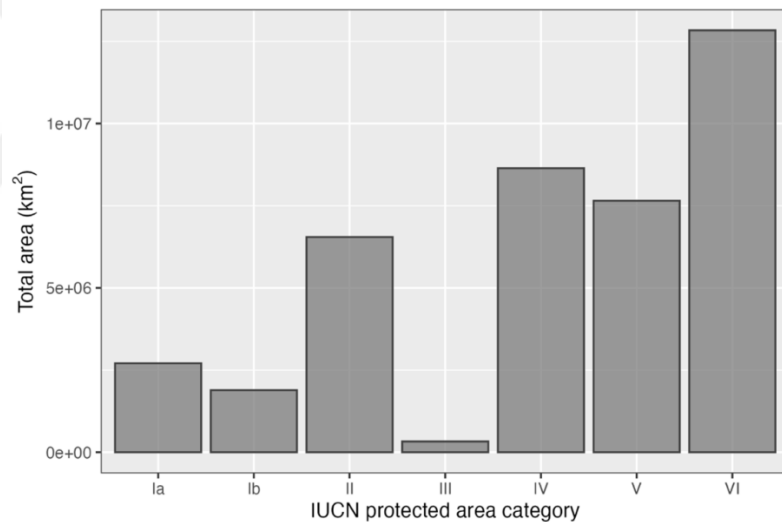


Figure 2.18 Total area of representation for each protected area category for the six categories defined by the International Union for Conservation of Nature in the study area.

The protected area categories differ substantially in the level of protection they offer (Dudley et al. 2010), which means their potential impact on community stability is possibly different. Furthermore, the effectiveness of protection for a category may also differ among different countries (Li et al. 2024). Despite these potential

problems, I decided to take a simplistic approach and included all categories of protected areas in my analyses, following published studies that pooled all the six categories to study effects of protected areas (e.g., Coetzee et al., 2014; Howard et al., 2023; Santangeli et al., 2022). Consequently, I pooled all protected areas belonging to the six categories to obtain a single protected area layer and calculated the total protected area (in km²) and proportional coverage in each study square.

As seen in Figure 2.18, the protected areas in the study area are dominated by lower-protection categories, such as categories IV, V, and VI (Dudley et al. 2010), which may render pooling all levels a bit counter-intuitive. However, I will suggest two additional lines of support to back this decision. First, most of the protected areas in Europe do offer at least some degree of protection (Jones-Walters and Čivić 2013). Second, a study that analyzed human impact in different types of protected areas found that the human impact is significantly lower than expected for category VI, which may suggest that even the lower-ranked categories are capable of delivering substantial levels of protection (Leroux et al. 2010). Therefore, I believe that all six categories can deliver some level of protection, and it is perfectly okay to pool them to study their effect, like it has been done in other studies (see above).

2.2.9.2.5 Land cover change

Given the importance of land cover change in shaping spatiotemporal patterns of biodiversity (Sala et al. 2000, Jantz et al. 2015, IUCN 2022, Montràs-Janer et al. 2024), I included it as a covariate in my community stability analyses. For this purpose, I utilized European Space Agency (ESA) - Climate Change Initiative (CCI) Global Land Cover (LC) product (ESA-CCI-LC), offering consistent annual global land cover maps at 300 m spatial resolution from 1992 to 2015. (CCI 2017). ESA-CCI-LC classifies land cover into 37 classes using a two-level hierarchical system with 22 first-level and 37 second-level classes. Table 2.7 lists the land cover classes in the dataset, their hierarchical class codes, as well as the corresponding broader

classes that Intergovernmental Panel on Climate Change (IPCC) uses in their change detection analyses.

Table 2.7 Descriptions of the land cover classes in the European Space Agency Climate Change Initiative global land cover (ESA-CCI-LC) dataset, their hierarchical class codes, and the corresponding broader classes used by Intergovernmental Panel on Climate Change (IPCC). Source: CCI (2017).

<i>Land cover class description</i>	<i>First level</i>	<i>Second level</i>	<i>IPCC</i>
No Data	0	0	
Cropland, rainfed	10	10	Agriculture
Herbaceous cover	10	11	Agriculture
Tree or shrub cover	10	12	Agriculture
Cropland, irrigated or post-flooding	20	20	Agriculture
Mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%)	30	30	Agriculture
Mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%)	40	40	Agriculture
Tree cover, broadleaved, evergreen, closed to open (>15%)	50	50	Forest
Tree cover, broadleaved, deciduous, closed to open (>15%)	60	60	Forest
Tree cover, broadleaved, deciduous, closed (>40%)	60	61	Forest
Tree cover, broadleaved, deciduous, open (15-40%)	60	62	Forest
Tree cover, needleleaved, evergreen, closed to open (>15%)	70	70	Forest
Tree cover, needleleaved, evergreen, closed (>40%)	70	71	Forest
Tree cover, needleleaved, evergreen, open (15-40%)	70	72	Forest
Tree cover, needleleaved, deciduous, closed to open (>15%)	80	80	Forest
Tree cover, needleleaved, deciduous, closed (>40%)	80	81	Forest
Tree cover, needleleaved, deciduous, open (15-40%)	80	82	Forest
Tree cover, mixed leaf type (broadleaved and needleleaved)	90	90	Forest
Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	100	100	Forest
Mosaic herbaceous cover (>50%) / tree and shrub (<50%)	110	110	Grassland
Shrubland	120	120	Shrubland
Evergreen shrubland	120	121	Shrubland
Deciduous shrubland	120	122	Shrubland
Grassland	130	130	Grassland
Lichens and mosses	140	140	Sparse vegetation
Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	150	150	Sparse vegetation
Sparse tree (<15%)	150	151	Sparse vegetation
Sparse shrub (<15%)	150	152	Sparse vegetation
Sparse herbaceous cover (<15%)	150	153	Sparse vegetation
Tree cover, flooded, fresh or brakish water	160	160	Forest
Tree cover, flooded, saline water	170	170	Forest
Shrub or herbaceous cover, flooded, fresh/saline/brakish water	180	180	Wetland
Urban areas	190	190	Settlement
Bare areas	200	200	Bare area
Consolidated bare areas	200	201	Bare area
Unconsolidated bare areas	200	202	Bare area
Water bodies	210	210	Water
Permanent snow and ice	220	220	

http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf contains the guidelines on how to download the data.

The reason why I preferred ESA-CCI-LC over other land cover datasets, such as the well-known CORINE Land Cover (CLC) product (EEA 2018) is that the other products either lacked data from several countries (e.g., the CORINE did not include

data from the mainland UK, Norway, Sweden, and Finland in its earliest available 1990 version; EEA, 1990) or lacked sufficient temporal coverage for my study period, such as the MODIS Land Cover (MCD12Q1) product (USGS 2018), which provides data for 2001 onwards. After reviewing nearly all available land cover products that provide data for the study area and period, I concluded that the ESA-CCI-LC product offered the best combination of spatial and temporal coverage. This product was also the dataset of choice in another study that studied range shifts in birds using the same atlas datasets used in this study (Howard et al. 2023). After downloading the land cover dataset, I processed it on R (R Core Team 2024), using the utilities of the *terra* (Hijmans 2024a), *raster* (Hijmans 2024b), and *sf* (Pebesma 2018) packages.

In my thesis, I considered a “before-after” approach, which assesses land cover change by comparing the land cover at the beginning and end of the study period, to quantify land cover change in the study squares. This method is widely used in land cover change analysis because it provides the most straightforward assessment of changes over time (Mausel et al. 2004, Lambin and Geist 2008). I quantified the change between the start (t_0) and end (t_1) periods for each study square by calculating the dissimilarity between the land cover at t_0 and t_1 using the Bray-Curtis dissimilarity or temporal beta diversity (Magurran and McGill 2011). This index of dissimilarity focuses on relative abundances, making it suitable for comparing samples of varying sizes such as the study squares, which may have different land masses due to the UTM grid structure or due to being located on coastal regions.

To calculate the temporal beta diversity or dissimilarity of land cover, I first constructed a site-by-land cover class matrix, where rows represent “before” and “after” states of a square and columns represent the 10 cover classes. I then defined the start year (i.e., EBBA1 survey year or t_0) and end year (i.e., EBBA2 survey year or t_1) for each country separately, to account for the differing survey dates for the countries involved in the atlases (see section 2.2.2). The start year was 1992 for all of the study squares as EBBA1 had been finalized before that date in all participating countries (see Table 2.2 in section 2.2.2.1). I then calculated the temporal Bray-

Curtis dissimilarity, which is aimed to serve as a proxy of land cover change, using the *bray.part* function in the *betapart* package (Baselga and Orme 2012). I deliberately designed my “before-after” approach to ignore the land cover class identities or diversity. This decision was based on (i) there are species that thrive even in the most unforgiving of the land use classes, such as urban areas or deserts (Dean and Williams 2004, Sayol et al. 2020a), and I expect every land cover class used in this study to be able to support some bird species; (ii) regardless of the nature and spatial distribution of land use or land cover change, I expect communities in a square to remain relatively more stable if the square does not experience much change in its land cover. While this approach overlooks habitat fragmentation, a known driver of changes in ecological communities (Sala et al. 2000, de Chazal and Rounsevell 2009, Mantyka-Pringle et al. 2015), quantifying fragmentation is a fairly complex process (Wang et al. 2014) which is why I wanted to avoid it in my land cover change analyses.

I also quantified a more straightforward land cover change measure by calculating the percentage of pixels that transitioned from one land cover class to another between EBBA1 and EBBA2. Here, I used percentages rather than the absolute number of pixels that changed to avoid any potential area-related effects.

Lastly, it is important to note that the land cover data used in this study, ESA-CCI-LC, only covers 24 years (from 1992 to 2015) of the 29-year study period (mainly from 1988 to 2017). This limitation means that, in this study, establishing any general relationship between the land cover change and community stability would be based on the assumption that land cover changes during the six years not covered by the ESA-CCI-LC data are comparable to the change from 1992 to 2015 in terms of intensity and spatiotemporal pattern.

2.2.9.2.6 Initial land cover diversity

Previous studies have found that landscape-scale habitat heterogeneity can influence temporal stability of bird communities (Hovick et al. 2015, García-Navas et al. 2021). To test the effect of initial land cover diversity on stability of bird communities, I utilized the ESA-CCI-LC land cover dataset (CCI 2017) and quantified Shannon's diversity index (Formula ; Magurran & McGill, 2011) for the corresponding years using the *diversity* function in *vegan* package (Oksanen et al. 2019) in R. Shannon's diversity index (H'), also referred to as Shannon's entropy, is a metric used to quantify the diversity within a community (Shannon 1948). The metric is widely used in ecology to assess species diversity (Magurran and McGill 2011, Magurran 2013). Shannon's diversity index accounts for both species richness and evenness, and it simply measures uncertainty associated with predicting the species identity of an individual randomly selected from a community (Shannon 1948, Magurran and McGill 2011).

$$H' = - \sum_{i=1}^S (p_i \ln (p_i)) \quad (2.5)$$

Shannon's diversity index, H' , is calculated by summing the products of relative abundances, p , and natural logarithm of those relative abundances for all species in a community with species richness S . A high value of H' indicates a diverse community having many species with relatively similar abundances, making it hard to predict the species of a randomly chosen individual (Krebs 2009, Magurran and McGill 2011). Since I aimed at calculating Shannon's diversity index for land cover in study squares, I simply replaced species with land cover classes and species abundances and relative abundances with the number and proportion of raster pixels present in each of the 37 land cover classes included in the study. I utilized the land cover data for the closest available years to the EBBA1 survey date for each square to calculate the initial land cover diversity, taking into account the different survey dates for the squares.

2.2.9.2.7 Climate change

It is a well-established fact that bird communities respond to changes in climate (La Sorte and Jetz 2010, Fogarty et al. 2020), and climate change remains one of the major threats for biodiversity (Pereira et al. 2010). Therefore, I decided to include climate-change-related variables in my analyses to assess the extent to which breeding bird community stability is affected by changing climate.

Research has shown that some bird species are more sensitive to changes in winter climate (Reif et al. 2010), while others are more responsive to changes in spring and summer climate (Fogarty et al. 2020, Virkkala et al. 2023), and some simply respond to changes in annual climate (Silleet et al. 2000, Morrison and Bolger 2002). The direction and strength of the responses also vary between habitats. For example, precipitation is expected to positively affect birds in arid and semi-arid regions (Iknayan and Beissinger 2018), while fitness of forest birds may respond negatively or not respond at all to changes in precipitation (Fogarty et al. 2020).

In this thesis, I chose to use temperature and precipitation to quantify changes in climate in the study squares because these variables are known to directly or indirectly influence fitness of a wide range bird species across a wide range of habitats (Bateman et al., 2016; Crimmins et al., 2011; Lawler et al., 2009; Root, 1988; VanDerWal et al., 2013), and they are commonly used in predicting occupancy and distribution of birds (Bateman et al., 2016; Milanesi et al., 2017). I utilized the WorldClim historical monthly weather dataset (Fick and Hijmans 2017), which provides global-scale data on monthly minimum and maximum temperatures as well as total precipitation for the period 1960-2021 period, with a finest spatial resolution of 2.5 arc minutes. The dataset is freely accessible at <https://www.worldclim.org/>.

I downloaded data for six decades, from the 1960s and 2020s. I then used the monthly weather data and the *biovars* function from the *dismo* package (Hijmans et al. 2023) to calculate the 19 BioClim variables. These bioclimatic variables are ecologically meaningful variables representing climatic trends, seasonality, and potential

environmentally limiting factors such as the minimum temperature in the coldest month (Fick and Hijmans 2017). Research has demonstrated that the BioClim variables can be effectively used in estimating bird species distributions on large scales, such as the one considered in this thesis (Bradie and Leung 2017, Milanese et al. 2017, Keller et al. 2020, Oliveira et al. 2021). Finally, I used the utilities of the *terra* package (Hijmans 2024a) to process the BioClim rasters in R (R Core Team 2024).

Given that bird species differ in their sensitivity to seasonal climatic conditions (see above), I chose a set of BioClim variables, each representing climatic conditions during different periods of the year. The variables I chose to capture the overall annual climatic conditions were BIO1 (mean annual temperature) and BIO12 (total annual precipitation). To represent climatic conditions in the summer, I utilized BIO10 (mean temperature of the warmest quarter) and BIO18 (precipitation of the warmest quarter), assuming the warmest quarter corresponds mostly to summer time in the study area (see section 2.2.1).

Considering the fact that climate tends to influence bird distributions over broad scales and over the long-term (Betts et al., 2019; Lemoine et al., 2007 - but also see Bateman et al., 2016; Reside et al., 2010, which suggest short-term climate may also perform well at predicting distribution of some birds), I chose to use a multi-year time window rather than annual snapshots when evaluating climate changes. For this purpose, I calculated the mean values for each of the six BioClim variables over the 10 years preceding the EBBA1 survey year to represent the climate for the first time step over the 10 years preceding the EBBA2 survey year to represent the climate for the second time step. This approach allowed me to capture long-term climatic conditions, which are generally more influential than the short-term climatic conditions in shaping bird distributions at a given site (Betts et al. 2019), for at each study square at the times of EBBA1 and EBBA2.

Given the apparent absence of concordance in responses of bird species to changes in climate, I quantified climate change not only in a directional manner (i.e.,

increases or decreases), but also in an absolute manner, focusing more on the amount of change rather than its direction. I analyzed three sets of BioClim variables representing different time periods: the annual set (BIO1 and BIO12), and the summer set (BIO10 and BIO18), and quantified the change for set separately. To achieve this, I first scaled and centered each BioClim variable and calculated 10-year averages for each time period (as described earlier). Next, I plotted the averaged values for each pair of BioClim variables (one temperature and one precipitation variable from each set) for the EBBA1 and EBBA2 periods in a 2D space, with one axis representing temperature and the other representing precipitation (Figure 2.19). Finally, I quantified the Euclidean distance between the EBBA1 and EBBA2 points in this 2D space to measure the shift in 10-year climatic conditions. Since this shift will always have a value greater than (if there is any change at all) or equal to zero, it effectively provides a non-directional way to quantify the change in temperature and precipitation in the study squares.

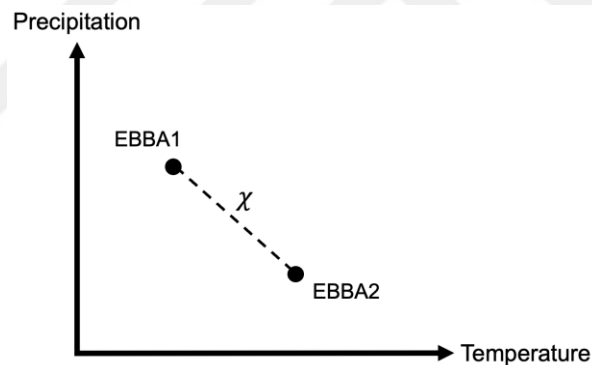


Figure 2.19 Illustration of the method used to quantify climatic shifts between the EBBA1 and EBBA2 periods. The 10-year-averaged values of a temperature-related BioClim variable (x-axis) and a precipitation-related BioClim variable (y-axis) are plotted for each period in a 2D climatic space. The Euclidean distance (χ) between the EBBA1 and EBBA2 points represents the magnitude of climate change.

2.2.9.2.8 Biome coverage

I included percent coverage of major terrestrial biomes in the study squares as a covariate in my analyses, as biomes and communities inhabiting them are facing different threats (Sala et al. 2000, Ellis et al. 2010). To test the effect of biome types on stability of breeding bird communities, I downloaded the widely-used terrestrial ecoregions of the world database of Olson et al. (2001), available in a high-resolution vector format at <https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world>, and processed it on Google Earth Engine (Gorelick et al. 2017) to calculate percent coverage of each biome in the study squares. This dataset defines 14 different biomes globally, which are based on the biome systems given in Ricketts et al. (1999) and World Wildlife Fund (1995). These biomes are tropical & subtropical moist broadleaf forests, tropical & subtropical dry broadleaf forests, tropical & subtropical coniferous forests, temperate broadleaf & mixed forests, temperate conifer forests, boreal forests, tropical & subtropical grasslands, savannas & shrublands, temperate grasslands, savannas & shrublands, flooded grasslands & savannas, montane grasslands & shrublands, tundra, Mediterranean forests, woodlands & scrub, deserts & xeric shrublands, and Mangroves (Olson et al. 2001). A close inspection of the biome map showed that only six of these biomes were represented in my study area: temperate broadleaf & mixed forests, temperate conifer forests, boreal forests, temperate grasslands, savannas & shrublands, tundra, and Mediterranean forests, woodlands & scrub (see section 2.2.9.2.8). Consequently, I only quantified the percentages of these biomes in my study squares.

2.2.9.2.9 Stabilizing dispersal potential

In the context of this thesis, immigrants belonging to the species that are already present in a community, or having similar functional traits to those already represented in the community can theoretically render a community compositionally or functionally more stable. It is intuitive to assume that high levels of dispersal

connectivity should act to homogenize the communities both taxonomically and functionally, as it prevents complete extinction of populations through colonizations, potentially promoting community stability (Valanko et al. 2015). In other words, the extinction of a species in a local patch can be compensated by arrival of individuals from the same species or with the same or similar trait values, thereby helping the community remain taxonomically or functionally stable, respectively. Considering the important roles that dispersal can potentially play in community stability, I decided to include it as a covariate in my thesis.

Dispersal is inherently difficult to quantify in natural systems, although technological advances in tracking technologies over the last decades have made it easier (Jönsson et al. 2016). This complexity makes understanding the effect of dispersal on structure and stability of interconnected communities challenging (Jacobson and Peres-Neto 2010). Adding to the complexity, the relationship between spatial beta diversity and dispersal rate is far from a straightforward linear relationship (e.g., Márquez et al. 2016, Lu 2021). Fortunately, experiments that allow for full control over individual movements between sites have provided some insight into this matter and demonstrated the homogenizing effect of dispersal on species composition, e.g., in plants and phytoplankton (e.g., Kneitel and Miller 2003, Guelzow et al. 2017). Additionally, studies conducted on natural systems have shown the stabilizing and recovery-contributing effects of dispersal in zooplankton and aquatic invertebrate (e.g., Gray and Arnott 2011, Valanko et al. 2015). To my knowledge, there are no published studies that directly addressed the impact of dispersal on the stability of bird communities.

Given all this information, I hypothesize that study squares surrounded by squares with taxonomically and functionally similar communities during the period of EBBA1 were able to remain taxonomically and functionally more stable due to their high stabilizing dispersal potential. I acknowledge that whether a dispersal event from one square to another occurs, and its outcome, will depend on many other factors, including climate, stochastic events, topography, geography (Davies et al. 2007, Matias et al. 2013, Weeks et al. 2023), and functional traits of the dispersing

bird species, such as their body mass, wing length, and wing shape (e.g., Habel et al. 2019, Pringle et al. 2019, Oliveira et al. 2019), as well as the dominant community assembly processes at the local scale (Márquez et al. 2016). However, for the sake of simplicity, I chose to quantify stabilizing dispersal potential for a focal square by adopting an island biogeography approach (IBT, MacArthur and Wilson 1967). I calculated the stabilizing dispersal potential as a function of mean pairwise taxonomic/functional similarity (measured as 1- total Sørensen's dissimilarity, representing stabilizing effect) between the focal square itself and its first-degree neighbors, along with the land surface area of the focal square and its first-degree neighbors (representing the area effect; Figure 2.20). I hypothesized that the larger land surface areas of squares with potential source populations (i.e., neighbors of a focal square, analogous to mainland in IBT) and the focal square (analogous to an island in the IBT) should promote repeated dispersal and colonization from the source populations (Losos and Ricklefs 2009, MacArthur and Wilson 1967, Wehr et al. 2023). Beyond the area effect, the distance of the focal square to a source is another factor known to impact the immigration rates (MacArthur and Wilson 1967, Losos and Ricklefs 2009, Pigot et al. 2020). A previous study that was conducted on the same dataset used in this thesis found that the average range shift for breeding bird species between the periods of EBBA1 and EBBA2 was 2.4 km/year, corresponding to 72 km over a 30-year period (median: 71 km with 95% CI: 6-638 km; Howard et al. 2023). Another recent study that focused on range shifts in breeding wetland birds found that the yearly range shift was only ~2 km per year between the periods of EBBA1 and EBBA2 (Soultan et al. 2022). Although species range shifts and dispersal are different ecological concepts, with the latter potentially leading to the former (Auer and King 2014, Howard et al. 2023), I still think range shift distances are relevant information sources on how far successful (in terms of establishment) movements of individuals between interconnected bird populations can be. As for dispersal distances, which are more relevant in the context of this thesis than the range shift distances, a recent study that utilized ringing data on 234 European bird species discovered that the mean annual dispersal distance is only a

few kilometers, with only a tiny fraction of species having dispersal distances greater than 10 km (Fandos et al. 2023). Based on the information provided in the three studies mentioned above, I opted to define the potential source populations for my study period (i.e., between EBBA1 and EBBA2) as the first-degree neighbors for each focal square. This is because the maximum distance from a point on the edge of a focal square to another point on the edge of one of its first-degree neighbors is ~70 km. Another reason for using only the first-degree neighbors and not a collection of, for example, the first, second, and third-degree neighbors is that, dispersal in birds, like many other organisms, is distance-dependent (Paradis et al. 1998, Sutherland et al. 2000, Garcia-R and Matzke 2021). Incorporating additional degrees of neighbors would require inventing a weighting scheme to account for distance-dependent dispersal potential, introducing further complexity, which I aim to avoid in my pursuit of a simplistic stabilizing dispersal potential index.

Finally, after deciding on the components of the index, which are taxonomic or functional similarity with the first-degree neighbors, land surface area of the neighbors, and land surface area of the focal square itself, I then developed a formula to calculate a stabilizing dispersal potential index for a focal square. The formula has the following features: (i) a higher taxonomic or functional similarity with the neighbors should be associated with higher index values (ii) a larger area of a neighbor should be associated with higher potential as a dispersal source (iii) a neighbor's individual potential as a stabilizing dispersal source should depend on how similar they are to the focal square and how large it is (iv) having a high number of neighbors should have a positive and additive effect on the index value (v) index value should range between [0, 1] to ease interpretability with higher values of the index implying higher stabilizing dispersal potential of the neighbors (Figure 2.20). The formula 2.6 satisfies all of these except for the last point, which will simply be achieved by rescaling the index (lower row in formula 2.6) values between [0, 1] at the cost of compatibility and comparability, which could easily be attained by skipping the rescaling step.

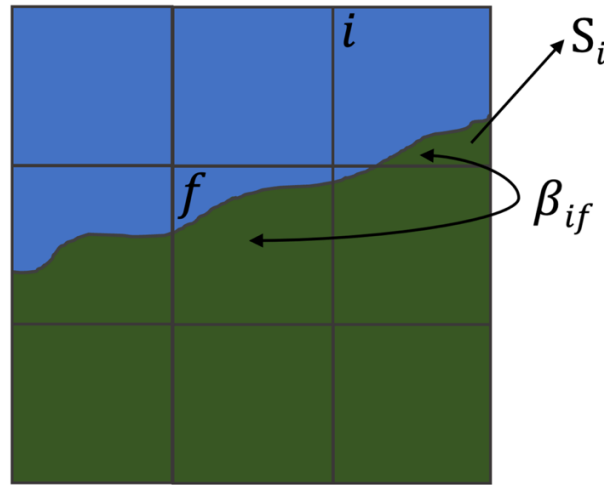


Figure 2.20 Stabilizing dispersal potential index D_S for a focal square f is a function of its taxonomic or functional dissimilarity (β_{if}) to its neighbors, the land surface areas of its neighbors (S_i), and the number of its neighbors (n). See formula 2.6 and for a detailed description of the relationship.

$$D_S = \sum_{i=1}^n ((1 - \beta_{if}) S_i) \quad (2.6)$$

$$D_{S_{scaled}} = \frac{D_S - D_{S_{min}}}{D_{S_{max}} - D_{S_{min}}}$$

Two examples demonstrating the application of this formula are given in Table 2.8. These examples effectively illustrate the additive nature of the index and show how a single neighboring square with a land surface area of $2S$ can offer the same level of stabilizing dispersal potential as two smaller squares, each with area S , as long as they are equally dissimilarity to the focal square.

Table 2.8 Hypothetical examples demonstrating how stabilizing dispersal index D_S works.

<i>Focal square</i>	<i>Neighbors</i>	<i>Areas of the neighbors (km²)</i>	<i>Total dissimilarity with the focal square</i>	<i>Ds (non-scaled)</i>
F1	N1	1000	0.5	500 + 500 = 1000
	N2	1000	0.5	
F2	N3	2000	0.5	1000

I calculated pairwise taxonomic and functional total beta diversity (β_{SOR} and $F_{\beta_{\text{SOR}}}$) for a focal square and each of its first-degree neighbors using R software (R Core Team 2024) and *beta.pair* and *functional.betapart.core* functions from the *betapart* package (Baselga and Orme 2012). Data for land surface area in each square was obtained by processing GTOPO30: Global 30 Arc-Second Digital Elevation Model (USGS 1996) on Google Earth Engine (Gorelick et al. 2017). Data processing and visualization on R were conducted using the *tidyverse* (Wickham 2017) and *sf* (Pebesma 2018) packages. I hypothesized that the communities with higher stabilizing potential index would remain more stable.

2.2.10 Statistical modeling

Autocorrelation is the lack of independence between pairs of observations that are at specific distances in time or space (Legendre 1993). This dependence between observations often violates the assumption of independence required by many commonly used statistical procedures, such as regression analyses (Legendre 1993, Kissling and Carl 2008). Spatial autocorrelation (SAC) is a specific form of autocorrelation involving dependence across geographic space, which is particularly common in ecological data (Diniz-Filho et al. 2003). SAC can bias standard regression models by introducing false positives, leading to inflated Type I errors (Diniz-Filho et al. 2003, Kissling and Carl 2008).

In this chapter of my thesis, I address SAV using a type of simultaneous autoregressive model (SAR; Anselin, 1988), specifically a spatial error model (SEM; Bivand, 2008; LeSage, 2008). SEMs are a special type of SAR models that account for spatial autocorrelation in the error term (Bivand, 2008). This approach is particularly useful when the spatially autocorrelated component is not fully explained by the included explanatory variables or when it arises directly from the response variable itself. To address this, a spatial error term is incorporated as a predictor (Formula 2.7; Kissling & Carl, 2008; Meynard et al., 2011).

$$\begin{aligned}
Y &= X\beta + \epsilon \\
\epsilon &= \lambda W\epsilon + v
\end{aligned}
\tag{2.7}$$

In this type of model, the response variable (Y) is defined as a function of the fixed effects of predictors included in the model ($X\beta$) and a spatial error term (ϵ). This error term, in turn, is determined by the spatial autocorrelation parameter (λ), which quantifies the strength of spatial dependence, the spatial weights matrix (W), which defines the neighborhood structure, and a random error term (v). Here, the term $W\epsilon$ indicates that the error at a given location is influenced by errors of neighboring locations. To fit the SEM models, I used the *errorsarlm* function from the *spdep* package (Bivand et al. 2005).

In my models, taxonomic and functional stability were the response variable, while the explanatory variables included the extrinsic and intrinsic variables presented in section 2.2.9, along with some interaction terms (see section 2.2.10.2 for detailed descriptions of structures of the models). I scaled and centered the explanatory variables before including them in the models, as this helps stabilize model estimations and mitigate collinearity issues (Zuur et al. 2010).

The response variables used in this study are naturally bounded within the [0, 1] interval and exhibit highly skewed distributions (section 2.2.8). Since SEMs assume normally distributed errors (Bivand 2008), the skewed nature of the response variables posed a challenge in achieving normally distributed errors or residuals. I assessed normality of the residuals visually using histograms and quantile-quantile (Q-Q) plots (Zuur et al., 2010). Unfortunately, the Q-Q plots consistently showed deviations from the 1:1 line at both extremes (Figure 2.21) in models using raw response variables.

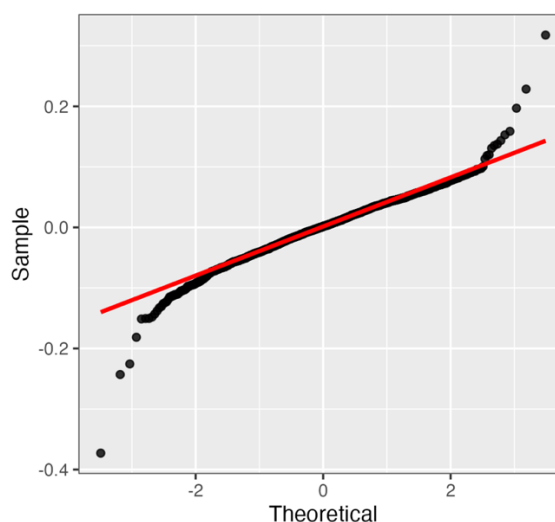


Figure 2.21 A normal quantile-quantile (Q-Q) plot for one of the linear models built for the functional stability response. The solid red line represents the 1:1 line, while the black dots represent observations.

In this study, I was unable to model the response variables using beta regression, which would have been the most appropriate approach to model these variables, as they are constrained within the $[0, 1]$ interval (Zeileis et al. 2010, Zuur et al. 2010). This limitation arose due to the presence of SAC, which could not be effectively accounted for SAC using spatial smoothers in generalized additive models (Wood 2017) or by including Moran's eigenvectors as predictors in generalized linear models (Kissling and Carl 2008, Zuur et al. 2009b, Brooks et al. 2017). Neither of these approaches successfully eliminated SAC in the model residuals. To assess the presence of SAC, I conducted Moran's I test using the *moran.test* function from the *spdep* package (Bivand et al. 2005) and additional diagnostic utilities from the *DHARMA* package (Hartig 2018b). Moran's I test is a widely used method for detecting spatial autocorrelation (Anselin 2002). The test statistic, Moran's I, which typically ranges from -1 to +1, where positive values indicate positive SAC (neighboring observations are more similar than expected under spatial randomness), negative values indicate negative SAC (neighboring observations are more dissimilar), while values close to zero suggest no spatial dependence (Moran 1950,

Anselin 1995). The test also provides a p-value, indicating the statistical significance of the observed SAC.

Since none of the aforementioned linear and non-linear modeling approaches successfully accounted for SAC, using beta regression was not a viable option for modeling the response variables in this chapter. Therefore, as an alternative, I utilized a Box-Cox transformation (Box and Cox 1964, Osborne 2010) to transform the response variables and help normalize the residuals in the SEM models. The Box-Cox transformation provides a data-driven method to select the best transformation and improve model assumptions (Osborne 2010). To determine the optimal transformation parameter for each response variable (taxonomic stability and functional stability), I used the *boxcox* function from the *MASS* package (R Core Team 2024). Additionally, I log-transformed two explanatory variables that had skewed distributions, mean elevation and percentage of protected area, to improve model stability and homoscedasticity (Zuur et al. 2009b, 2010). The structure of the final global models I fitted are given in section 2.2.10.1.2.

In the SEM models I fitted, I used the *k*-nearest neighbor (KNN) method to define the neighborhood structure. In this method, the neighborhood structure for each study cell is defined based on its *k* closest neighbors, ensuring that every individual study unit has exactly *k* neighbors, regardless of the actual physical distances between the units (Anselin 2002). This method is particularly effective in areas with variable spatial density, as it prevents isolated observations from having no neighbors (Getis and Aldstadt 2004).

2.2.10.1 Neighborhood structure of the SEM models

Selecting the optimal number of *k* neighbors in the KNN method is crucial when constructing the spatial weights matrix, as it directly influences model performance, spatial autocorrelation, and subsequent statistical inference (Anselin 1988, 2002). The primary function of the spatial weights matrix (*W* in formula 2.7) in SEM

models is to capture spatial relationships, ensuring that observations account for their neighboring influences. If k is too low, the spatial structure may fail to adequately capture spatial dependence, leading to an incomplete representation of spatial relationships (Getis and Aldstadt 2004). Conversely, if k is too high, it may artificially impose spatial relationships between observations that are not actually spatially dependent. This can lead to biased parameter estimates and over-smoothed spatial relationships (Fotheringham and Rogerson 2013).

Previous studies suggest that the optimal k neighbors can be chosen using data-driven methods. It is generally recommended to experiment with different k values and assess model performance using various criteria, such as Akaike Information Criterion (AIC; Burnham & Anderson, 2002) and Moran's I (Meynard et al. 2011, Kubara and Kopczewska 2024). AIC is a widely used metric for statistical model selection that balances model fit and complexity by measuring how well a model explains the data while penalizing excessive model complexity to prevent overfitting (Burnham and Anderson 2002). Among a set of competing models, the one with the lowest AIC score is considered the best, as it optimally balances goodness-of-fit and parsimony (Burnham and Anderson 2002, Anderson et al. 2011). In this study, I adopted a hybrid approach, incorporating multiple metrics to determine the optimal k . In addition to AIC and Moran's I, I also evaluated mean absolute error (MAE), calculated using the spatial block k -fold cross validation method (Pohjankukka et al. 2017, Roberts et al. 2017). This allowed for a robust assessment of model performance across different values of k in defining the spatial neighborhood structure.

Here, I aimed to detect an optimal k value with (i) Moran's I value as close to zero as possible, indicating minimal SAC, (ii) a low AIC score, ensuring a good balance between goodness-of-fit and complexity, and (iii) a low MAE, minimizing prediction error and reducing the risk of overfitting.

To achieve this, I calculated AIC, Moran's I (along with its p-value), and MAE for each k value between 4 and 40, incrementing by two for the global model, which

included all candidate variables. Selecting the optimal number of k neighbors should be performed using the global model, as conducting model selection before determining k may lead to the premature elimination of variables that could be important in the final model but appear less significant under a suboptimal k . Furthermore, AIC is only comparable across SEM models that use the same spatial weight matrix (Burnham and Anderson 2002, Bivand 2008). Since AIC-based model selection, which I employed in my analyses (section 2.2.10.1.2), relies on likelihood calculations that depend on the spatial structure, it cannot be applied across candidate models fitted using different k values. Such models would be incomparable in terms of AIC, as their likelihood estimates are determined by distinct spatial neighborhood definitions (Bivand 2008).

Across the range of the tested k -nearest neighbor values, the results indicated that the study area, covering Europe and Iceland, naturally splits into two disconnected spatial components or sub-graphs: one for the mainland European region and the UK, and another for Iceland across the tested k value. This occurs because Iceland is geographically isolated from the European mainland, and the KNN method inherently preserves the nearest-neighbor structure within contiguous spatial clusters.

Table 2.9 presents the Moran's I values, their associated p -values, AIC scores, and MAE for each k value tested during the selection process for the SEM models fitted to taxonomic and functional stability responses.

Table 2.9 Moran's I values, corresponding p-values, mean absolute error (MAE) (calculated using k -fold spatial block cross-validation), and Akaike Information Criterion (AIC) for the k -neighbor values tested in the taxonomic stability (left) and functional stability (right) models. Gray-highlighted cells indicate the optimal values for each metric. Asterisks (*) denote the selected k -neighbor value.

k	Moran's I	p-value	MAE	AIC	k	Moran's I	p-value	MAE	AIC
4	-0.05786	0.99993	0.02595	-12779.78	4	-0.02384	0.93964	0.02182	-9300.36
6	-0.03890	0.99919	0.02588	-12877.83	6	-0.02041	0.94895	0.02191	-9346.73
8	-0.03679	0.99968	0.02580	-12897.45	8	-0.01629	0.93138	0.02198	-9357.99
10	-0.02900	0.99861	0.02580	-12913.00	10	-0.01442	0.92820	0.02202	-9367.32
12	-0.02327	0.99564	0.02579	-12929.53	12	-0.01474	0.94964	0.02218	-9357.03
14	-0.01798	0.98496	0.02573	-12939.98	14	-0.01353	0.94720	0.02227	-9353.93
16	-0.01401	0.96377	0.02572	-12948.63	16	-0.01184	0.93433	0.02237	-9350.47
18	-0.01080	0.92715	0.02567	-12951.25	18	-0.01052	0.92169	0.02244	-9348.64
20*	-0.00725	0.84317	0.02565	-12954.93	20*	-0.00642	0.81185	0.02250	-9359.59
22	-0.00645	0.82438	0.02570	-12948.76	22	-0.00384	0.70031	0.02253	-9359.51
24	-0.00641	0.83329	0.02573	-12946.88	24	-0.00308	0.66448	0.02259	-9360.80
26	-0.00703	0.86721	0.02575	-12935.31	26	-0.00278	0.65173	0.02255	-9354.61
28	-0.00583	0.82735	0.02582	-12937.17	28	-0.00195	0.60223	0.02256	-9353.16
30	-0.00545	0.81788	0.02584	-12933.53	30	0.00021	0.44977	0.02255	-9354.40
32	-0.00397	0.74474	0.02590	-12933.36	32	0.00229	0.30015	0.02260	-9357.33
34	-0.00416	0.76344	0.02599	-12925.18	34	0.00364	0.21029	0.02257	-9356.84
36	-0.00418	0.77087	0.02614	-12918.39	36	0.00271	0.26060	0.02255	-9344.43
38	-0.00370	0.74665	0.02638	-12915.99	38	0.00235	0.27942	0.02253	-9339.02
40	-0.00373	0.75438	0.02665	-12910.62	40	0.00199	0.30042	0.02248	-9333.40

The results of the model selection procedure showed that none of the tested k values produced significant spatial correlation, suggesting that the SEM models effectively accounted for spatial autocorrelation (SAC) within this range (Table 2.9). The MAE values remained relatively stable across the tested k -values, with the difference between the lowest and highest MAE being less than 3% in all cases. In contrast, AIC values did vary in this range of k -values, with few to several best AIC values in the tested range for the two models.

Based on these findings, I selected 20 as the optimal number of k -neighbors for both models, as it offered a balanced trade-off among the performance metrics. This choice implies the spatial dependence operate at the level of the 20 nearest neighbors. At this k value, MAE values were 11% of the range of both response variables and were consistently smaller than their standard deviation. While AIC score of the

functional stability model was not the lowest at the $k = 20$ level, this k -value produced a Moran's I value that was 2.25 times smaller than that of the model with the lowest AIC, supporting its selection.

2.2.10.2 Backward selection

I used backward model selection to identify the most significant predictors in the SEM models. This approach starts with a global model, a model that includes all candidate variables, and iteratively removes the least significant predictors based on the p -values, until all remaining variables meet a predefined significance level, which was $\alpha = 0.05$ in this study (James et al. 2013). This approach offers several advantages, including improved model interpretability, thanks to the presence of fewer variables, reduced risk of overfitting, and computational efficiency (Hastie et al. 2009, Harrell 2015).

Although I did not include correlated variables in the same models, I checked for multicollinearity by using variance inflation factors (VIF; O'brien, 2007) in the global models, prior to conducting the model selection. I did not include in the models, explanatory variables that had correlation coefficients larger 0.50 or smaller than -0.50. Nevertheless, I checked VIF in every model by using the *vif* function from the *car* package (Fox and Weisberg 2018). VIF is an important quantity, as it reflects an estimate of the degree of interrelationship or multicollinearity of an explanatory variable with other explanatory variables in a model (Marcoulides and Raykov 2019). The VIF threshold I set was 5, which is a lot more conservative than the commonly suggested threshold of 10 (O'brien 2007). I started eliminating the variables with the highest VIF value in the global models until every variable has $VIF < 5$. Formulae of the global models after this elimination process are given below.

Taxonomic stability

$$\begin{aligned}
&= \beta_0 + \beta_1(\log \text{mean elevation}) + \beta_2(\log \text{protected area}) \\
&+ \beta_3(\text{biome5}) + \beta_4(\text{biome6}) + \beta_5(\text{biome8}) + \beta_6(\text{biome11}) \\
&+ \beta_7(\text{biome12}) + \beta_8(\text{land cover dissimilarity}) \\
&+ \beta_9(\text{initial land cover diversity}) \\
&+ \beta_{10}(\text{land cover pixel change}) \\
&+ \beta_{11}(\text{temp. \& prec. change in the warmest quarter}) \\
&+ \beta_{12}(\text{temp. \& prec. change in the warmest quarter}) \\
&+ \beta_{13}(\text{annual temp. \& prec. change}) + \beta_{14}(\text{BIO1}) \\
&+ \beta_{15}(\text{BIO10}) + \beta_{16}(\text{BIO12}) + \beta_{17}(\text{BIO18}) \\
&+ \beta_{18}(\text{tax. dispersal potential}) \\
&+ \beta_{19}(\text{initial species richness}) + \beta_{20}(\text{time gap}) + \epsilon
\end{aligned} \tag{2.8}$$

Functional stability

$$\begin{aligned}
&= \beta_0 + \beta_1(\log \text{mean elevation}) + \beta_2(\log \text{protected area}) \\
&+ \beta_3(\text{biome4}) + \beta_4(\text{biome5}) + \beta_5(\text{biome6}) + \beta_6(\text{biome8}) \\
&+ \beta_7(\text{biome11}) + \beta_8(\text{initial land cover diversity}) \\
&+ \beta_9(\text{land cover pixel change}) \\
&+ \beta_{10}(\text{temp. \& prec. change in the warmest quarter}) \\
&+ \beta_{11}(\text{annual temp. \& prec. change}) + \beta_{12}(\text{BIO1}) \\
&+ \beta_{13}(\text{BIO1}) + \beta_{14}(\text{BIO10}) + \beta_{15}(\text{BIO12}) + \beta_{16}(\text{BIO18}) \\
&+ \beta_{17}(\text{func. dispersal potential}) + \beta_{18}(\text{time gap}) \\
&+ \beta_{19}(\text{initial FOri}) + \beta_{20}(\text{initial FDis}) + \beta_{21}(\text{initial FDiv}) \\
&+ \beta_{22}(\text{initial Rstar}) + \beta_{23}(\text{initial FDis: initial FNND}) + \epsilon
\end{aligned} \tag{2.9}$$

β_0 : Intercept

β_n : Regression coefficients

Biome4: Temperate broadleaf & mixed forests

Biome5: Temperate conifer forests

Biome6: Taiga

Biome8: Temperate grasslands, savannas, and shrublands

Biome11: Tundra

Biome12: Mediterranean forests, woodlands, and scrub

Temp.: Temperature

Prec.: Precipitation

BIO1: Mean annual temperature

BIO10: Mean temperature of the warmest quarter

BIO12: Annual precipitation

BIO18: Precipitation of the warmest quarter

FDis: Functional dispersion

FDiv: Functional divergence

FOri: Functional originality

FNND: Functional nearest neighbor distance

Rstar: Functional redundancy (R^* or Rstar)

See sections 2.2.9 for a detailed description of the explanatory variables, their ecological relevance, and sources I used to extract the data.

I used an AIC-based approach to perform backward selection (Burnham and Anderson 2002). At each step of the model selection, after I removed the least significant variable, refit the model, and assessed improvements in model fit using the $\Delta AIC < 2$ rule. This rule states that models within two AIC units of each other are considered statistically equivalent in terms of goodness-of-fit and complexity (Burnham and Anderson 2002). When the improvements in AIC were less than two units of AIC, I considered the model with fewer terms as the better model. According to the principle of parsimony, simpler models should be preferred over more complex ones unless there is strong evidence that the additional complexity provides a significant improvement in explanatory power (Burnham and Anderson 2002,

Anderson et al. 2011). This is because simpler models are generally more robust, easier to interpret, and less prone to overfitting (Gauch Jr 2002, Hastie et al. 2009).

I chose not to perform model averaging across the best models with $\Delta AIC < 2$. While model averaging is a useful tool for addressing model uncertainty, it can be problematic when applied to models with interaction terms, which were present in the functional stability model (Burnham and Anderson 2002, Heinze et al. 2018). As noted by Burnham and Anderson (2002) and (Cade 2015), interaction terms are highly context-dependent and sensitive to the specific set of predictors included in the model. Furthermore, while AIC-based multi-model inference is useful, selecting a single best model is often preferable when one model outperforms others in terms of interpretability and simplicity (Gauch Jr 2002, Burnham and Anderson 2002). For these reasons, I selected a single best model for each of the two global models, and reported results exclusively from those models (see above).

2.2.10.3 Model validation

I validated the SEM models by inspecting their residuals to ensure that model assumptions were met (Bivand 2008, Zuur et al. 2009b). First, I visually inspected the residual distribution using a histogram and a Q-Q plot. A valid model is expected to have normally distributed errors and observations closely following the 1:1 line in the Q-Q plot. I also employed the Kolmogorov-Smirnov test of normality on the residuals by using the *ks.test* function from the *stats* package (R Core Team 2024) to formally test for their normality. Second, I plotted residuals against fitted values. A valid model's residuals are expected to be randomly distributed around zero, showing no discernible patterns, and their variance should remain consistent across the range of fitted values. Third, although I initially checked for multicollinearity in the global models, I reassessed VIF values for the selected models as well (section 2.2.10.1.2). Lastly, I assessed the predictive performance of the models using two types of k-fold cross validation. First, I employed standard k-fold cross validation, where the dataset is randomly divided into k blocks or subsets. The model is trained

using all subsets except one, which is then used for validation (Stone 1974). Then, the process is repeated for each subset. However, this method might lead to overly optimistic error estimates if there is spatial dependence in the data (Pohjankukka et al. 2017, Roberts et al. 2017). To account for spatial autocorrelation (SAC), I also used spatial k-fold cross-validation (also known as spatial block k-fold cross-validation) (Pohjankukka et al. 2017, Roberts et al. 2017). In this approach, the dataset is partitioned into spatially contiguous blocks rather than random subsets. Cross-validation is then performed using these blocks, reducing optimistic bias in error estimates caused by SAC. I defined spatial blocks using the *spatialBlock* function from the *blockCV* package (Valavi et al. 2019) to define the spatial blocks, setting a maximum block distance of 150 km, approximately three times the study unit size (50×50 km). This distance was chosen to capture spatial autocorrelation at a meaningful scale while ensuring sufficient independence between training and testing data (Roberts et al. 2017).

To account for spatial autocorrelation (SAC), I also used spatial k-fold cross-validation (also known as spatial block k-fold cross-validation) (Pohjankukka et al., 2017; Roberts et al., 2017). In this approach, the dataset is divided into spatially contiguous blocks rather than random subsets. Cross-validation is then performed using these blocks, reducing optimistic bias in error estimates caused by SAC. I defined spatial blocks using the *spatialBlock* function from the *blockCV* package (Valavi et al., 2019), setting a maximum block distance of 150 km—approximately three times the study unit size (50×50 km). This distance was chosen to capture spatial autocorrelation at a meaningful scale while ensuring sufficient independence between training and testing data (Roberts et al., 2017).

At the end of the cross validation steps, I quantified mean absolute errors (MAE) to assess predictive performance of the models. MAE is a natural measure of error that measures the deviation for each prediction (Willmott and Matsuura 2005). Unlike root mean square error (RMSE), MAE is purely a measure of error; that is, it is a function errors themselves alone. RMSE, on the other hand, is a function of errors as well as distribution of errors and number of errors, which may compromise its

accuracy in evaluation of model performance (Willmott and Matsuura 2005, Hyndman and Koehler 2006).

When I evaluated the model residuals of the final models, I found no violation of modeling assumptions. The residual distributions and Q-Q plots indicated no apparent departures from normality (Bivand 2008). Similarly, the Kolmogorov-Smirnov Test confirmed that the residuals did not significantly deviate from a normal distribution. Finally, a visual inspection of the residuals versus fitted and residuals versus the predictors suggested no apparent heteroskedasticity issue in the selected models (Zuur and Ieno 2016). The model diagnostic plots can be found in Appendix B.2.

A thorough discussion of the statistical methods used in this chapter is provided in Appendix B.3.

2.3 Results

The results of my analyses showed changes in the community weighted mean (CWM) of the four key traits considered, some of which were in unexpected directions. Additionally, both the taxonomic and functional stability of the study communities were influenced by a combination of intrinsic and extrinsic factors. In the following sections, I present these results in detail.

2.3.1 Changes in community weighted means of key traits

CWM changes of key traits showed mixed results. CWM changes in body mass occurred mostly in the form of increases across the study area, with a slight positive mean (Figure 2.22a and Figure 2.23a). Changes in CWM of the relative brain mass trait were mostly negative, although there were regions of increases in southeast and northernmost part of the study area (Figure 2.22b and Figure 2.23b). Changes in CWM of the breeding in grassland habitat trait showed a mixed pattern, with zones

of increases and decrease, although the mean changes across the region was nearly zero (Figure 2.22c and Figure 2.23c). Changes in CWM of the percentage of invertebrates in breeding season were characterized by widespread declines in the region (Figure 2.22d and Figure 2.23d).

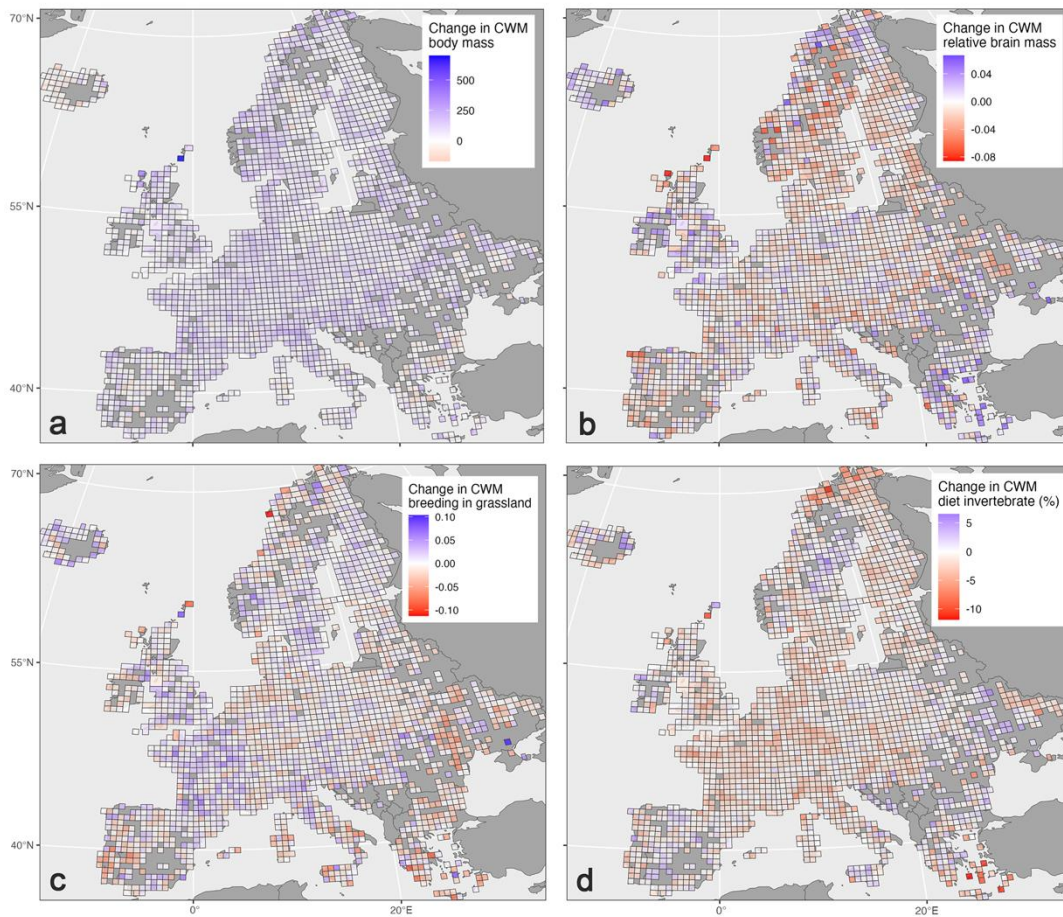


Figure 2.22 Changes in community weight means (CWMs) of four key traits across the study area: (a) body mass, (b) relative brain mass, (c) breeding in grassland habitats, and (d) percentage of invertebrates in breeding season diet. The body mass trait was measured in grams. The relative brain mass trait uses residualization to break the allometric relationships it has with body mass. The breeding in grassland habitat was a binary-coded trait and CWM values represent the ratio changes in birds species using grassland habitats. See section 2.2.4 for more information on these traits.

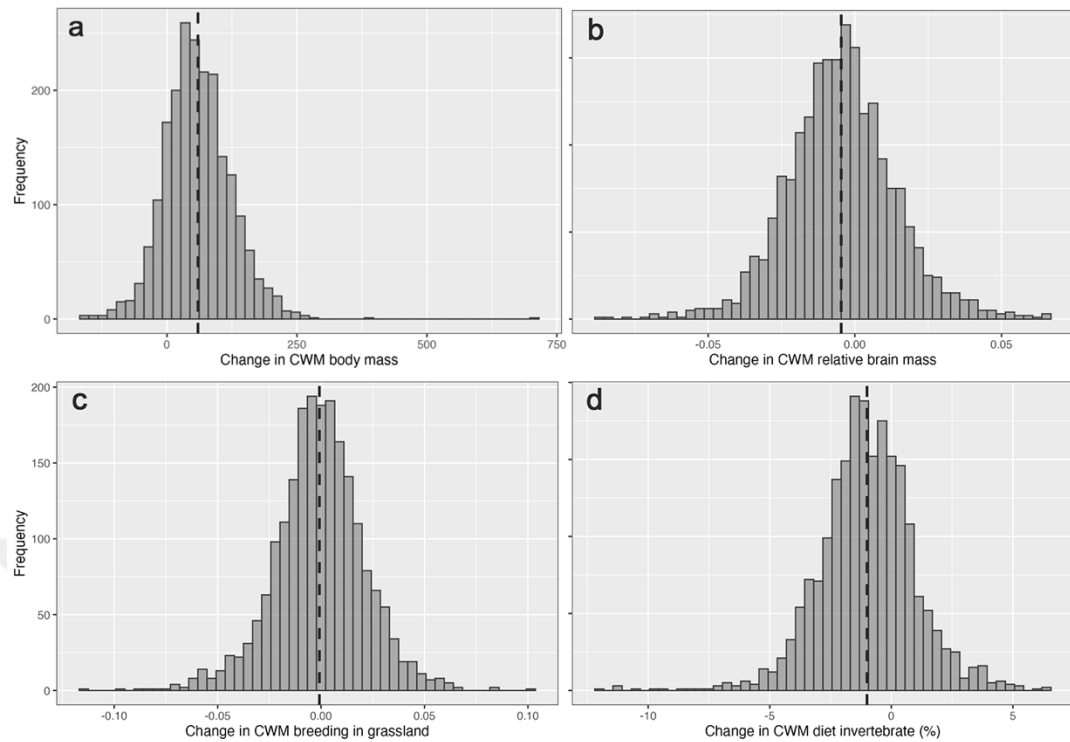


Figure 2.23 Distributions of changes in community weight means (CWMs) of four key traits across the study area: (a) body mass, (b) relative brain mass, (c) breeding in grassland habitats, and (d) percentage of invertebrates in breeding season diet. The body mass trait was measured in grams. The relative brain mass trait uses residualization to break the allometric relationships it has with body mass. The breeding in grassland habitat was a binary-coded trait. See section 2.2.4 for more information on these traits.

To gain further insight into the reasons behind the rather unexpected changes in the body mass and relative brain mass traits, I turned my attention to species with the highest numbers of extinctions and colonizations. Figure 2.24 gives scientific names, as well as their body mass and relative brain mass rankings of the top 10 species with the highest number of colonizations and extinctions between the EBBA1 and EBBA2 periods.

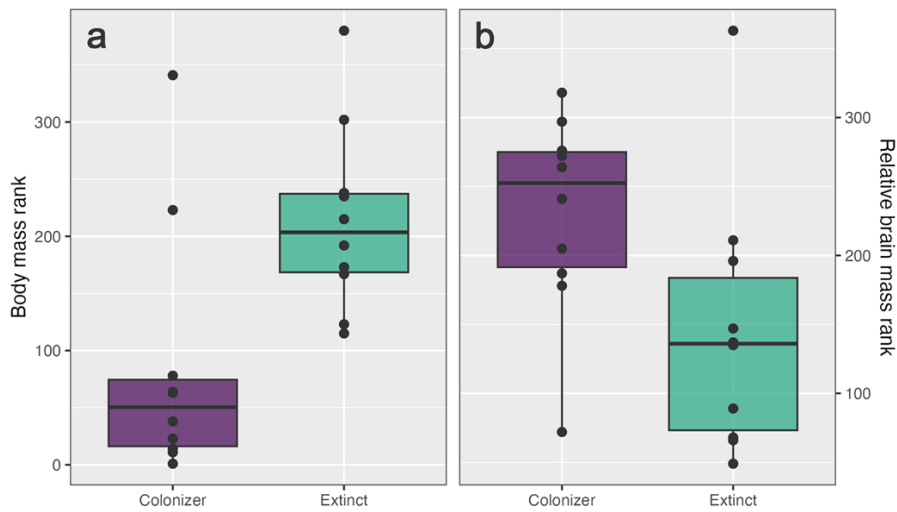


Figure 2.24 (a) Body mass and (b) relative brain mass rankings of the top 10 species with the highest numbers of colonization and extinctions. Lower numbers indicate higher rankings.

Unexpectedly, species that colonized higher numbers of squares over the study period were the ones with larger bodies (Figure 2.24a) and smaller relative brain sizes (Figure 2.24b). The full lists of the top 10 species with the highest numbers of colonization and extinctions are provided in Appendix B.5.

2.3.2 Community stability

Both of the final models had several variables following the backward selection procedure. In the following sections, I give further information on the results of the model selection and validation steps, and present output of the final models.

2.3.2.1 Taxonomic stability

Overall, taxonomic stability during the study period was high, with a mean value of 0.88 (SD = 0.05). Lower taxonomic stability values were observed towards the northern and southeastern edges of the study area (Figure 2.25).

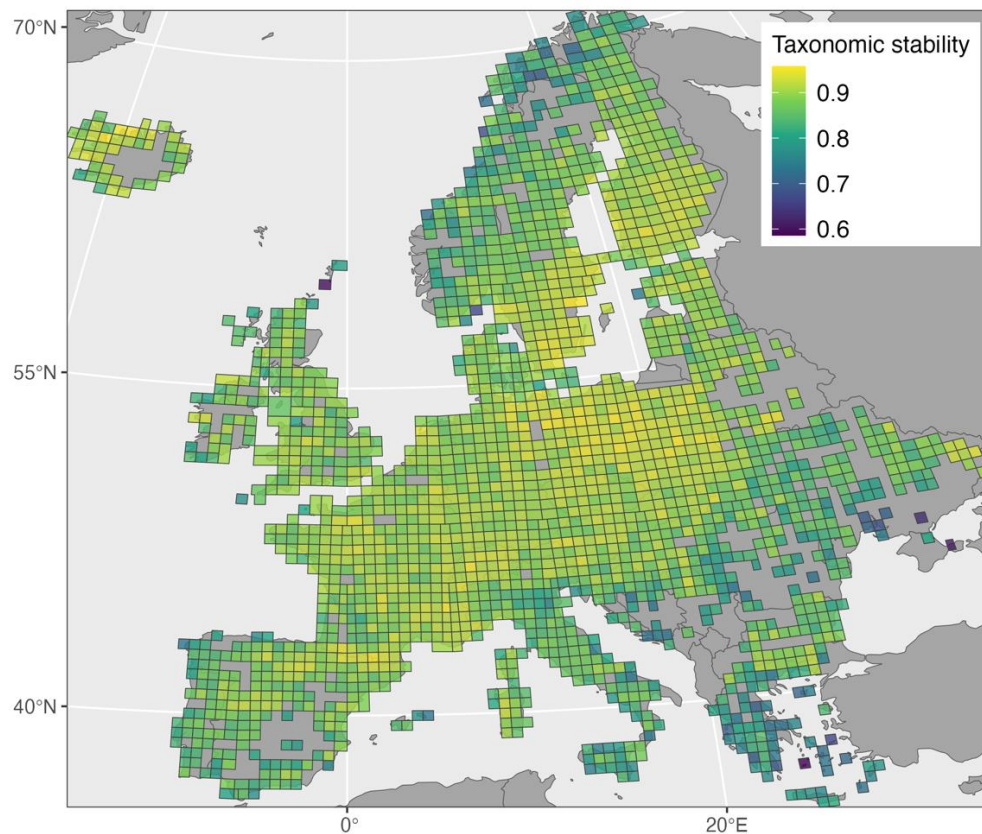


Figure 2.25 Taxonomic stability of the study squares over the study period, calculated as temporal taxonomic beta diversity.

Several extrinsic variables and initial species richness had significant effects on taxonomic stability. Model results indicate that squares experiencing greater annual temperature change over the study period had significantly lower taxonomic diversity (Figure 2.26 and Table 2.10). Being located in the Mediterranean or Tundra biomes was associated with reduced taxonomic stability, whereas the opposite was observed for squares in the temperate conifer forest biome. As expected, an increase in protected area coverage provided a significant advantage in terms of taxonomic stability. Furthermore, squares with higher mean elevation, higher values of the taxonomically stabilizing dispersal potential index, and greater initial species richness were both associated with increased temporal taxonomic stability.

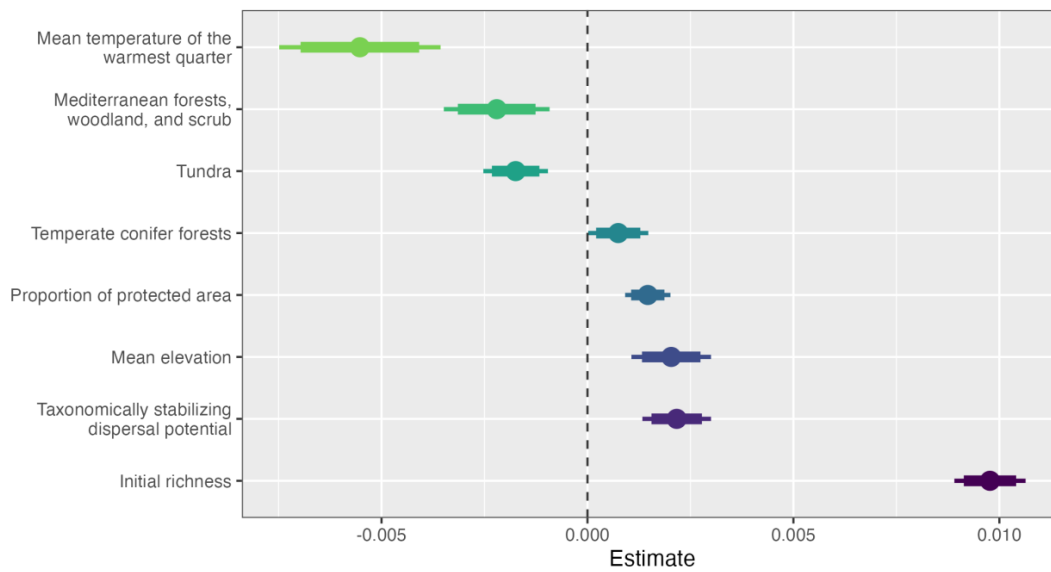


Figure 2.26 Effect size estimates (points) with their 95% (thinner error bars) and 85% (thicker error bars) confidence intervals for predictors included in the best spatial error models of taxonomic stability. The dashed line represents zero effect size. Explanatory variables have all been scaled prior to fitting the model.

Table 2.10 Effect size estimates, standard errors, and the upper and lower limits of the 95% and 85% confidence intervals (CI), along with significance levels (at the more conventional $\alpha = 0.05$ level) for the predictors included in the best spatial error models of taxonomic stability.

<i>Covariate</i>	<i>Estimate</i>	<i>Std. error</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>	<i>Lower 85% CI</i>	<i>Upper 85% CI</i>	<i>p-value (stars)</i>
(Intercept)	-0.0785	0.0017	-0.0818	-0.0752	-0.0809	-0.0761	< 0.0010***
Mean temperature in the warmest quarter	-0.0055	0.0010	-0.0075	-0.0036	-0.0070	-0.0041	< 0.0010***
Mediterranean forests, woodland, and scrub	-0.0022	0.0007	-0.0035	-0.0009	-0.0031	-0.0013	< 0.0010***
Tundra	-0.0017	0.0004	-0.0025	-0.0010	-0.0023	-0.0012	< 0.0010***
Temperate conifer forests	0.0007	0.0004	0.0000	0.0015	0.0002	0.0013	0.0450*
Proportion of protected area	0.0015	0.0003	0.0009	0.0020	0.0011	0.0019	< 0.0010***
Mean elevation	0.0020	0.0005	0.0011	0.0030	0.0013	0.0027	< 0.0010***
Taxonomically stabilizing dispersal potential	0.0022	0.0004	0.0013	0.0030	0.0016	0.0028	< 0.0010***
Initial species richness	0.0098	0.0004	0.0089	0.0106	0.0091	0.0104	< 0.0010***

Total temporal taxonomic dissimilarity was dominated by the turnover component, which had a mean value of 0.08 (~67% of the total dissimilarity) across the study squares, while the average nestedness-resultant dissimilarity was only 0.04 (~33% of the total dissimilarity).

2.3.2.2 Functional stability

The average functional stability of the study communities between the EBBA1 and EBBA2 periods was 0.88 (SD = 0.06). Similar to taxonomic stability, lower functional stability values were observed in southeastern parts of the study area. However, the rest of the region exhibited high variation in functional stability, with some low values also appearing in central continental Europe (Figure 2.27).

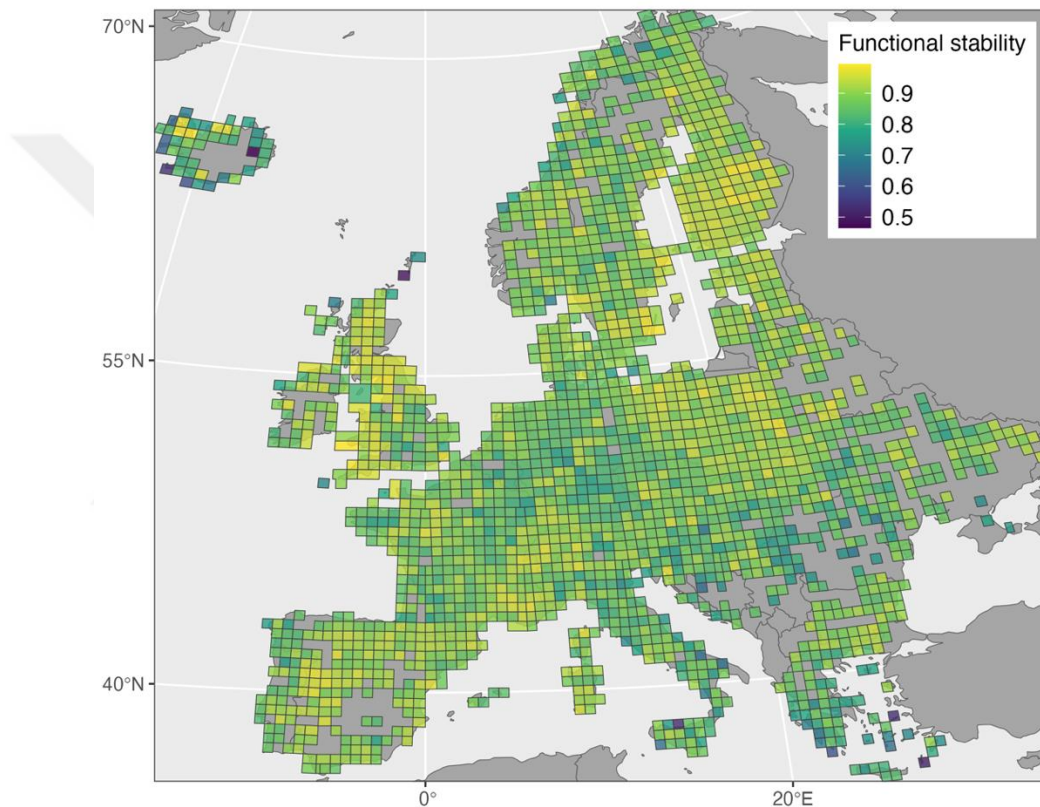


Figure 2.27 Functional stability of the study squares over the study period, calculated as temporal functional beta diversity.

Several initial functional diversity metrics and few extrinsic variables had significant effects on the spatial variation of the functional stability. Among the functional diversity measures included in the best model, initial functional divergence (FDiv) was the only functional diversity measure that was associated with lower functional stability (Figure 2.28 and Table 2.11). As expected, the effect of functionally

stabilizing dispersal potential was positive, though relatively weak. Interestingly, the effect of changing annual temperatures and precipitation on functional stability was positive. The temperate conifer forests biome coverage was the only biome-related covariate retained in the final model, and it had a significant positive effect on functional stability, consistent with its effect on taxonomic stability. Similarly squares at higher mean elevations exhibited significantly greater functional stability over the study period. Additionally, functional originality (FOri), functional redundancy (Rstar), and FDis all had positive impact on the temporal functional stability of the study communities.

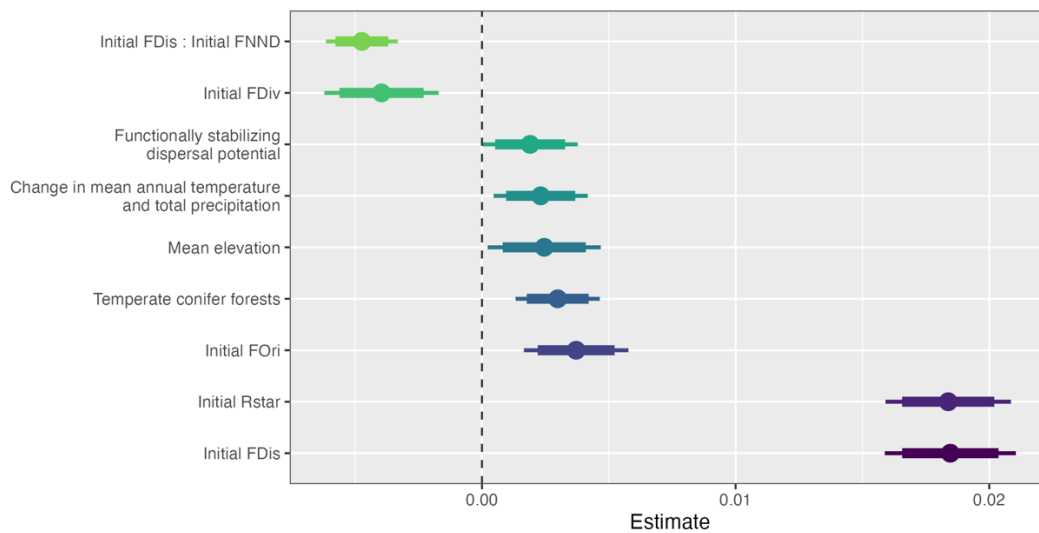


Figure 2.28 Effect size estimates (points) with their 95% (thinner error bars) and 85% (thicker error bars) confidence intervals for predictors included in the best spatial error models of functional stability. The dashed line represents zero effect size. Explanatory variables have all been scaled prior to fitting the model.

Table 2.11 Effect size estimates, standard errors, and the upper and lower limits of the 95% and 85% confidence intervals (CI), along with significance levels (at the more conventional $\alpha = 0.05$ level) for the predictors included in the best spatial error models of functional stability.

<i>Covariate</i>	<i>Estimate</i>	<i>Std. error</i>	<i>Lower 95% CI</i>	<i>Upper 95% CI</i>	<i>Lower 85% CI</i>	<i>Upper 85% CI</i>	<i>p-value (stars)</i>
(Intercept)	-0.0932	0.0024	-0.0980	-0.0884	-0.0967	-0.0897	< 0.0010***
Initial FDis : Initial FNND	-0.0047	0.0007	-0.0062	-0.0033	-0.0058	-0.0037	< 0.0010***
Initial FDiv	-0.0040	0.0012	-0.0062	-0.0017	-0.0056	-0.0023	< 0.0010***
Functionally stabilizing dispersal potential	0.0019	0.0010	0.0000	0.0038	0.0005	0.0033	0.0474*
Change in mean annual temperature and total precipitation	0.0023	0.0009	0.0005	0.0042	0.0010	0.0037	0.0114*
Mean elevation	0.0025	0.0011	0.0002	0.0047	0.0008	0.0041	0.0309*
Temperate conifer forests	0.0030	0.0008	0.0013	0.0046	0.0018	0.0042	< 0.0010***
Initial FOr	0.0037	0.0011	0.0017	0.0058	0.0022	0.0052	< 0.0010***
Initial Rstar	0.0184	0.0013	0.0159	0.0209	0.0166	0.0202	< 0.0010***
Initial FDis	0.0185	0.0013	0.0159	0.0210	0.0166	0.0204	< 0.0010***

Figure 2.29 shows how the effect of initial functional dispersion (FDis) varies across initial functional nearest neighbor distance (FNND) in relation to functional stability.

The effect size estimate for the interaction between initial FDis and FNND was negative, suggesting that higher FNND values reduce the positive effect of FDis on functional stability (Figure 2.28).

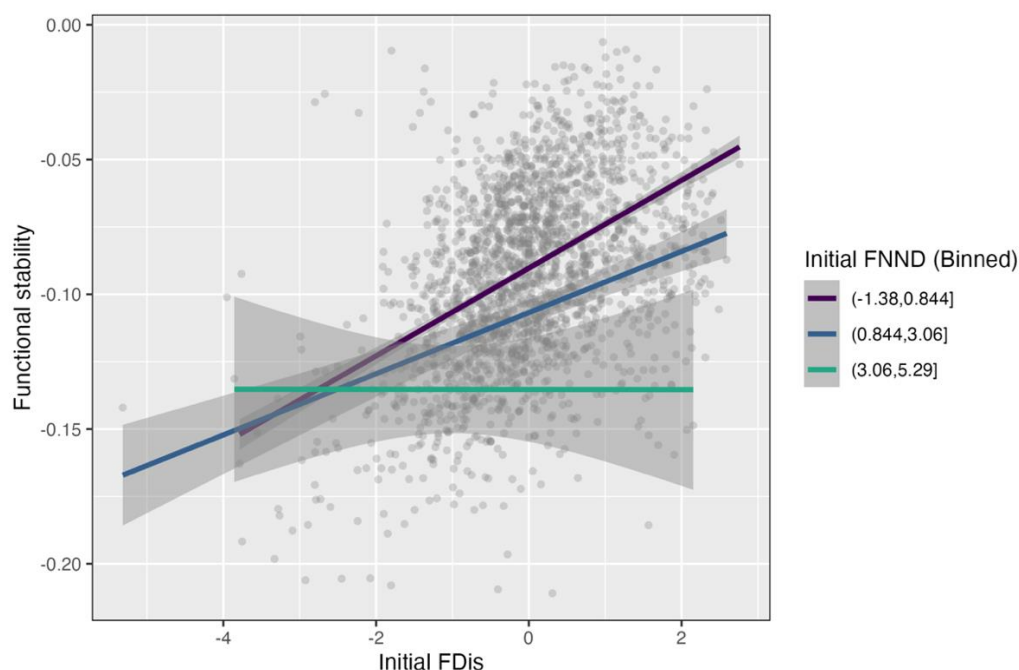


Figure 2.29 The interaction between initial functional dispersion (FDis) and initial functional nearest neighbor distance (FNND) in relation to functional stability. Solid lines represent regression lines fitted across three different FNND levels (in ascending order from top to bottom), shaded areas represent 95% confidence intervals around the estimated relationships, and gray points indicate individual observations. Both variables have been scaled prior to fitting the model.

Unlike its taxonomic counterpart, total functional dissimilarity was primarily driven by the nestedness component, which had a mean value of 0.07 across the study area. The average turnover-resultant functional dissimilarity was 0.05.

2.4 Discussion

This section discusses changes in the community-weighted means of the four key traits, along with the results of analyses identifying the extrinsic and intrinsic factors associated with community stability. Additionally, dedicated subsections examine the contributions of individual components of beta diversity to the observed

dissimilarity and provide a critical evaluation of the methods used to quantify community stability in this chapter.

2.4.1 Changes in key functional trait community weighted means

Contrary to my expectations, I observed a slight overall increase in body mass and slight decrease in relative brain mass (Figure 2.22). When I examined the lists of top 10 species (Appendix B.5) with the highest numbers of colonizations and extinctions more closely, I realized that among the species with the highest number of extinctions was the Ortolan Bunting (*Emberiza hortulana*), which is threatened by agricultural intensification and human activities such as hunting and trapping (Hagemeijer and Blair 1997, IUCN 2024). Another species with a high number of extinctions was Crested Lark (*Galerida cristata*), which is threatened primarily by agricultural intensification and pesticide use (de Juana et al. 2022, Howard et al. 2023, IUCN 2024). Among the top 10 species with the highest numbers of colonizations was the Peregrine Falcon (*Falco peregrinus*), whose populations have been increasing in Europe due to effective conservation efforts, high ecological tolerance, and restorative management in some parts of the study area (White et al. 2024). Another notable colonizer was the Great Cormorant (*Phalacrocorax carbo*), which has colonized or recolonized extensive areas in Europe as a result of effective protection measures, pesticide control, and reduced direct persecution over the past decades (Hatch et al. 2020). Mute Swans (*Cygnus olor*), the heaviest bird among the species included in this study, were also among the top 10 colonizers. Their range expansions and population size increases have been attributed to factors, including banning of lead shots and fishing weights, introduction efforts, and effective legal protection across much of Europe (Wood et al. 2024).

Larger body size has been associated with elevated extinction risk in birds and other organisms (Ripple et al. 2017), although the association can be threat-dependent (Chichorro et al. 2019). Previous studies have attributed the increased risk of extinction in larger-bodied animals to intrinsic factors such as lower reproductive

rate and output (Gaston and Blackburn 1995, Cardillo 2003), or extrinsic factors such as a tendency to be hunted or exploited more intensively (Whytock et al. 2016, Ripple et al. 2017). A larger body size can also be a thermoregulatory disadvantage in birds given the widespread warming in the region (Gardner et al., 2011; but also see Salewski et al., 2014). Despite these potential drawbacks, there was a slight increase in overall body mass across the study region, which may be attributed to well-targeted conservation and reintroduction efforts acting as unnatural evolutionary forces. Apparently, loss of small-bodied farmland species and colonization of large-bodied species with the help of conservation effects resulted in an overall increase in CWM of body mass in this study.

Higher relative brain mass in birds has been associated with higher population stability and an increased ability to cope with habitat changes and respond to novel environments (Sol et al. 2005, Shultz et al. 2005, Fristoe et al. 2017). Urbanization, which has been widespread in Europe (Kuemmerle et al. 2016), has been shown to favor larger-brained birds as well (Sol et al. 2020). However, a global review found that birds with smaller brains can also cope with or tolerate urbanization if they distribute their breeding events throughout the year as an alternative evolutionary strategy (Sayol et al. 2020b). Furthermore, some studies have reported declines in relative brain sizes of the grassland birds in Europe, attributing this trend to the homogenization and simplification of agricultural habitats (Guerrero et al. 2024). These factors, along with human interventions such as targeted-trapping, which can act as unnatural evolutionary forces, might explain the slight decrease in relative brain mass observed over the study period.

Contrary to my expectations, the overall change in CWM of the breeding in grassland habitat was nearly zero. In my view, this may be because of two main reasons. First, although existing grasslands face a wide range of threats, including agricultural expansion and intensification (e.g., Habel et al. 2013, Ambarlı et al. 2016), grassland conversion and ecological improvement have also occurred in some parts of Europe due to factors such as land abandonment and the adoption of high nature-value farming practices (Reidsma et al. 2006, Cramer et al. 2008, Kuemmerle et al. 2016).

Second, the breeding habitat trait itself is a non-mutually exclusive trait, meaning that a species can have more than one type of breeding habitat (see section 2.2.4). As a result, if a species breeds in grasslands as well as other habitats, it may still persist in the landscape even if grassland habitats deteriorate. This implies that an alternative trait that focuses specifically on grassland specialization might have yielded different results.

Changes in the community weighted means (CWMs) of the insectivory trait were in line with my expectations. Widespread declines in insect biomass and diversity have been reported from across the world, including Europe (van Klink et al. 2020, Finn et al. 2023). Studies on birds have consistently detected parallel declines in insectivorous bird populations (e.g., Møller 2019, Bowler et al. 2021), suggesting that insect declines may be driving the declines in insectivore birds. Furthermore, most of the insectivorous species in Europe are migratory (del Hoyo et al. 2018), and migratory species are often declining faster due to the wider range of threats they face (Sanderson et al. 2002). Further studies focusing exclusively on the driving forces behind these declines is recommended to help mitigate the ongoing loss of insectivorous bird populations.

I acknowledge that a deeper understanding of the changes in CWMs of the four key traits presented here deserves a more thorough discussion and, certainly, further analyses. However, since identifying and presenting the changes in CWMs of these traits was a rather minor aim of this chapter, I refrained from conducting further analyses to explore potential associations with other factors, such as changes in land use patterns. Such an endeavor would require its own dedicated chapter and would certainly be an interesting topic for future research.

2.4.2 Community stability

In the following sections, I discuss the findings related to the taxonomic and functional stability of the study communities in detail.

2.4.2.1 Contribution of turnover and nestedness components to total temporal beta diversity

Taxonomic compositional changes in breeding bird communities were primarily driven by species turnover, whereas functional changes were mainly due to the functional nestedness of communities between the EBBA1 and EBBA2 periods (section 2.3.2). The turnover-dominated temporal taxonomic beta diversity implies that differences between time points are primarily driven by species replacements (i.e., local extinctions and colonizations; Baselga 2010). In contrast, the nestedness-dominated temporal functional beta diversity suggests that communities recorded in EBBA2 period were functionally subsets of the communities of EBBA1 or vice versa (Baselga 2010, Baselga et al. 2015). Here, the functional composition of communities remained relatively stable, with changes in functional volume occupied being primarily driven by the loss or gain of species that did not significantly alter the overall functional space. This suggests that the colonizing species tended to be functionally similar to those that they replaced, maintaining the overall functional structure of the communities despite taxonomic replacements. Such a pattern has been observed in previous studies (e.g., Robroek et al. 2017), and it may arise if species with similar ecological roles are replacing each other, potentially due to environmental filtering and functional redundancy within the community. Nevertheless, the accompanying functional turnover suggests that species turnover occasionally led to the loss of previously occupied niches or the occupation of newly formed ones.

The contrasting patterns of taxonomic and functional beta diversity presented here highlight the importance of simultaneously utilizing both taxonomic and functional approaches simultaneously to gain a better understanding of the changes occurring in ecological communities. When considered together, these results provide a more comprehensive view that may not be evident when results from either one of the approaches are evaluated in isolation (Si et al. 2016, de Bello et al. 2021b).

2.4.2.2 Intrinsic factors

2.4.2.2.1 Initial species richness

Species richness was the only taxonomic diversity index used in this study due to data limitations (section 2.2.9.1). The results showed initial species richness was positively related to stability of breeding bird communities over the study period (Figure 2.26 in section 2.3.2.1), which aligned with my hypothesis. Several explanations could account for this pattern.

One possible explanation relates to how temporal beta diversity was calculated in this study. In this chapter, I used Sørensen's dissimilarity (section 2.2.8; Magurran and McGill 2011) to quantify temporal taxonomic beta diversity for the study communities. This index is sensitive to species richness present in the communities, meaning that if the same number of species is added or removed in two communities with different richness levels, the one with lower richness will exhibit a higher Sørensen's dissimilarity value and thus lower stability. This potential artifact is evident from the formula 2.2 (section 2.2.8), and it may partially explain the positive relationship observed between initial richness and taxonomic stability. The second explanation I offer concerns ecological mechanisms underlying the diversity-stability hypothesis. According to the diversity-stability hypothesis (MacArthur 1955, Johnson et al. 1996), as community diversity increases, the stability of ecosystem processes or community attributes are also expected to increase. Higher species richness can contribute to stability through increased interactions that help maintain ecosystem processes and species coexistence (MacArthur 1955, Elton 1958, McNaughton 1977, Dell et al. 2019b). Additionally, diverse communities may exhibit asynchronous responses, which can weaken the competitive interactions and contribute to stability (Jiang et al. 2024). A combination of these factors likely contributed to the positive effect of initial species richness on community stability. This result also aligns with previous studies reporting positive relationships between

species richness and stability (Tilman et al. 2006, Hillebrand et al. 2008, Mikkelsen et al. 2011, Blowes et al. 2019).

2.4.2.2.2 Initial functional diversity

The results showed that several functional diversity metrics of the initial communities had a significant impact on functional stability of the study communities. In this section, I will discuss these findings and their underlying mechanisms.

A key consideration in the analysis was the inclusion of functional redundancy indices, R and R_{star} (section 2.2.9.1). Including both indices simultaneously in the models was problematic, as they are both designed to quantify functional redundancy within communities (Ricotta et al. 2016, Pavoine and Ricotta 2019). Therefore, I selected R_{star} for the global model of functional stability, because this measure may be superior to R by accounting for the different levels of taxonomic and functional diversity in communities (Pavoine and Ricotta 2019). As expected, the results of the model showed that communities with higher initial functional redundancy exhibited significantly higher functional stability (Figure 2.28 in section 2.3.2.2). This intuitive positive relationship can be primarily attributed to the well-known insurance hypothesis (Naeem 1998, Yachi and Loreau 1999). This hypothesis posits that biodiversity provides stability to ecological systems by ensuring the persistence of ecological functions despite species losses due to environmental fluctuations (Yachi and Loreau 1999). One of the key mechanisms behind this hypothesis is functional redundancy, which points to the presence of multiple species with similar functional roles in a community (Naeem 1998, Mori et al. 2013, Biggs et al. 2020). In such communities, if one species declines or is lost, another with similar traits can compensate, maintaining functional stability. The idea presented here aligns with the redundancy hypothesis discussed in section 2.1.1, which states that in communities with high functional redundancy, loss of a few species can be compensated without significant change to the ecosystem processes or community properties (Walker

1992, Naeem 1998). These mechanisms can explain why squares with high functional redundancy may have better resisted changes in their functions due to species losses. However, the effect of species additions on functional stability is harder to predict. Regardless of the level of redundancy, newly added species may be functionally distinct from the existing community, altering the functional convex hull and potentially reducing functional stability. Whether a colonizing species modifies the convex hull likely depends on other community properties, such as functional richness (FRic; Villéger et al. 2008), rather than functional redundancy alone. However, if the redundancy is caused by environmental filtering dominating the community assembly, the establishing species would likely be functionally similar to the ones already present in the community, which would not change the stability much. Nevertheless, the functional insurance provided by high redundancy was evidently strong enough to yield a significant positive effect on functional stability. The positive relationship observed in this study is consistent with previous findings, which report increased functional stability in communities with higher functional redundancy (e.g., Leigh et al., 2019; Oliveira & dos Anjos, 2022).

I expected a non-linear, unimodal relationship between FDis and functional stability. However, I was unable to model this variable as a smooth term because spatial error models (SEMs; Anselin 1988, Bivand 2008) used in this chapter do not allow for smooth terms. Instead, the linear FDis term included in the model showed a significant and positive relationship with functional stability, suggesting that communities with higher initial FDis remained functionally more stable over the study period (Figure 2.28 in section 2.3.2.2). FDis measures the mean distance of species to the centroid of the community in functional space (Laliberté and Legendre 2010). High FDis indicates that species are widely spaced within the occupied functional space, maximizing trait divergence and minimizing clustering near the centroid. Additionally, FDis can increase if species are positioned toward the edges of the entire possible functional space, as long as they are well-distributed within the occupied space (Laliberté and Legendre 2010). Considering the fact that I relied on convex-hull-based hypervolumes for quantifying temporal functional stability

(section 2.2.8), it becomes evident that a community with high FDis could remain functionally stable simply because it would be less likely for a new colonizer to have trait values falling outside the extensive convex hull occupied by the community. Regarding species losses, a similar methodology-based approach would suggest lower functional stability because of the high trait divergence. However, from an ecological perspective, a community with a diverse set of response traits (see Table 2.6 in section 2.2.4 for the trait list) and a high FDis, is expected to exhibit enhanced resistance to environmental fluctuations due to niche complementarity and resource partitioning (Tilman 1999). Such a community also tends to have more relaxed competitive interactions and more asynchronous species responses to environmental perturbations, both of which can enhance community stability (Goldwasser and Roughgarden 1993, McCann 2000, Jiang et al. 2024). In my view, a combination of the factors mentioned here could explain the positive relationship between FDis and functional stability. Furthermore, initial FDis was found to be positively correlated with two other functional diversity metrics, FRic (Villéger et al. 2008) and Rstar (functional redundancy; Pavoine and Ricotta 2019). This suggests that the observed positive effect of FDis may be partially driven by the positive effects of FRic and Rstar on functional stability. Although I did not conduct any specific test to disentangle effects of these three functional diversity measures, higher values of FDis are apparently associated with higher values of FRic and Rstar, and the results presented here should be interpreted with this in mind.

I was unable to test the effect of initial FRic on functional stability, as this variable was strongly and significantly correlated with many other variables, including FDis and Rstar, both of which were included in the final functional stability model (Table 2.11 in section 2.3.2.2). Due to this collinearity and the absence of a clear directional hypothesis regarding its effect on functional stability, I chose to exclude FRic from the global model. However, I did include an interaction term for the interaction term for FRic and Rstar, which is discussed in the following passages.

As I hypothesized, initial functional divergence (FDiv; Villéger et al. 2008) was negatively associated with functional stability in this study (Figure 2.28 in section

2.3.2.2). In an incidence-based context, FDiv measures the degree to which species are positioned away from the centroid of the trait space, near the edges of the convex hull (Villéger et al. 2008a, Mouchet et al. 2010). It is maximized when all the species are located on the convex hull and at equal distance from the centroid (Villéger et al. 2008a). This suggests that communities with higher values of FDiv tend to have species near or on the edge of the functional space occupied by the community, which can theoretically render them susceptible to pronounced changes in convex hull following species losses. This because the lost species will more likely be one of the vertices of the convex hull, and consequently, its loss will alter the convex hull, reducing functional stability. This may well be what happened to the communities with high initial FDiv. I do not expect FDiv to influence to whether species additions will alter the convex hull or not, as such effects would more likely depend on shape and volume of the convex hull (Villéger et al. 2008a). However, initial FDiv still achieved a significant negative impact on temporal functional stability, likely due to the increased vulnerability of convex hull to structural changes following species losses.

The results showed the communities with higher initial functional originality (FOri; Mouillot et al. 2013) had higher functional stability (Figure 2.28 in section 2.3.2.2). This finding contradicted my earlier expectations. Community-level FOri measures functional distance of each species in a community to its nearest neighbor in the entire species pool, averaged across all species in the focal community (Mouillot et al. 2013, Magneville et al. 2022). This suggests that, a community with high FOri likely contains species that are isolated within the functional space, with no similar counterparts in the entire species pool. In such cases, I would expect species additions or losses to have a higher probability of distorting the convex hull occupied by the community by adding or removing vertices, thereby reducing functional stability. This hypothesis also holds from an ecological perspective, as the loss of functionally original bird species is a well-documented phenomenon (e.g., Devictor et al., 2008; Liang et al., 2019 - also see Chapter 1 on this thesis). However, these expected outcomes were not observed in this study. Since FOri is meaningful only

when the entire species pool is considered, I will comment on what the observed negative relationship means at the study area level. In my opinion, the observed positive relationship can be attributed to ecological distinctness of the species causing higher community-level F_{ori} in these communities. Communities with high F_{ori} have more functionally original or distinct species (Mouillot et al. 2013). This suggests that species in this community may face lower competition because their ecological roles are distinct. In theory, this can lead to more stable coexistence due to complementarity, where species use resources differently, and enhance community stability (Frost et al. 1995, McCann 2000). Although

As I hypothesized, initial functional specialization (F_{spe}; Bellwood et al. 2005, Mouillot et al. 2013) of a community was not associated with its functional stability. This is likely because community-level F_{spe} quantifies the distance of each species in a community to the centroid of the global species pool, averaged across all species in a community (section 2.2.9.1). This means that F_{spe} is defined with respect to the entire species pool, and it does not convey any information on the positioning of species within the functional space with respect to each other, which may be an important determinant of community stability (Walker 1992, Naeem 1998, Biggs et al. 2020).

Of the four interactions I analyzed (section 2.1.3.1), only the interaction between F_{dis} and functional nearest neighbor distance (F_{NND}; Weiher et al. 1998) had a significant influence on functional stability of the study communities (Figure 2.28 in section 2.3.2.2). This “deadly cocktail” is achieved in communities where species are located far from each other and from the centroid of the occupied functional space (Laliberté and Legendre 2010). In my opinion, such a trait dispersion pattern may result from limiting similarity dominating the community assembly process (MacArthur and Levins 1967, Herben and Goldberg 2014). In such communities, loss of a species would more likely cause pronounced changes in the convex hull of the community due to the lack of redundancy. Regarding species colonizations, if

limiting similarity dominates the community assembly following initial environmental filtering (Özgencil et al. 2020), I would expect the colonizing species to have distinct functional trait values, further altering the convex hull and reducing functional stability. As a consequence, the stabilizing effect of FDis would diminish at higher values of FNND, which was exactly what the results showed. This finding suggests that the positive effect of FDis on functional stability may rely on the presence of small functionally distinct clusters of species, rather than a uniform dispersion of species throughout functional space.

The analyses revealed no significant relationships between the FRic-Rstar, FDiv-Rstar, and FEve-FNND interactions and functional stability. The FRic-Rstar interaction may not have been significant due to the moderate positive correlation between the two indices (Spearman's rho: 0.64, $p < 0.001^{***}$). This correlation suggests that higher values of FRic are already associated with higher Rstar values, reducing the independent variability of Rstar. As a result, lower Rstar values may not be sufficiently represented at high FRic levels, limiting the ability to assess their interactive effect on functional stability. This might be what happened with the FDiv-Rstar case too, where a weaker positive correlation was observed (Spearman's rho: 0.37, $p < 0.001^{***}$). In my opinion, a combination of high FDiv and low Rstar combination would constitute an extremely “deadly cocktail” in terms of functional stability. However, this hypothesis remains to be tested with further data, potentially in other ecological systems. Lastly, the FEve-FNND interaction failed to achieve significance, likely because neither of these indices confer information about the volume occupied within the functional space. This means that, although the combination of high FEve and low FNND can, in theory, render a community resistant to changes in its convex hull due to species losses, it would not necessarily confer any stability advantage or disadvantage regarding species additions. This might be the reason why this interaction did not make it to the final model during the model selection process.

2.4.2.3 Extrinsic factors

2.4.2.3.1 Time gap and country identity

I hypothesized that the time gap between the EBBA1 and EBBA2 surveys would have a significant effect on the community stability of breeding birds in Europe. However, neither of the final models included this variable. In my opinion, this may be due to a few reasons. First, in this chapter, quantification of the time gap between the consecutive atlas surveys was carried out at the country level, as the survey date data was available only at this scale (section 2.2.2). This meant that all atlas squares within a given country had the same survey dates, were assigned the same survey dates, even though, in reality, survey timing likely varied across different squares (Hagemeijer and Blair 1997, Keller et al. 2020). Additionally, survey dates for countries were provided as intervals, and I used the midpoint of each interval to represent the survey date, which may have reduced representative accuracy further. Second, the modeling strategy I used may not have been well-suited for capturing the effect of time gap. Initial data exploration had suggested that there may be a non-linear relationship between stability and time gap. However, the spatial error models (SEMs; Anselin 1988, Bivand 2008), used in this study do not allow for smoothers. As a result, I was only able to test quadratic terms for exploratory purposes, and these did not indicate significant associations with community stability. Nevertheless, I recommend future studies to try models allowing for smoothers, such as generalized additive models (Wood 2017), to test the effect of time gap on community stability.

Lastly, time gap itself might not be an important predictor of community stability, simply because the pace at which other variables, such as land cover change (Kuemmerle et al. 2016), vary significantly across the study region. This means that time gap may only become a significant predictor when analyzed in combination with other influential variables in the same model. Considering these points, I recommend repeating the analyses by using generalized additive models (to define smoothers for the variable if needed) with the exact survey dates for each square,

which were not available to me. It seems highly likely that a time gap variable constructed using the exact survey years for each square would be an important predictor of both taxonomic and functional stability of breeding bird communities. This expectation is based on the assumption that communities observed over shorter intervals are expected to exhibit smaller changes in their taxonomic or functional composition (Lehman et al. 2000, Ives et al. 2003).

Initial data exploration and previous literature suggested that country identity could be an important predictor of community stability in this study. This is because countries in the study area differ in their nature conservation approaches (Jones-Walters and Čivić 2013) and the survey methods used in data collection (Hagemeijer and Blair 1997, Keller et al. 2020). However, the country identity variable was eliminated early in the modeling process due to high collinearity. This outcome was expected in the case of SEM models, which account for spatial dependence. Given this, and the fact many other variables included in the global models were also spatial in nature, such as the climatic variables (section 2.2.9.2), the country variable was removed early in the process. Since identifying the effect of country identity and differences between the countries in terms of the stability of their bird communities were not among objectives of the study, I refrained from conducting further analyses to explore the effect of this variable.

2.4.2.3.2 Mean elevation

The results showed that the mean elevation of a study square was positively associated with both taxonomic and functional stability of its breeding bird communities. This contrasted my expectation that mean elevation would have no effect on stability due to positive and negative influences cancelling each other out (section 2.1.3.3). In my view, the observed positive relationship between mean elevation of a square and the stability of its communities can be attributed to two major reasons. First, the squares with higher mean elevation may also provide a wider range of elevations. To test this hypothesis, I calculated elevational standard

deviation for each square using the same dataset, GTOPO30: Global 30 Arc-Second Digital Elevation Model (USGS 1996), as a measure of elevational variability. I found that standard deviation of elevation was positively, strongly, and significantly correlated with mean elevation across the study squares (Spearman's rho: 0.81, p -value < 0.001***), which led me conclude that the squares with higher mean elevation were also exhibited higher elevational variability. This suggests that these squares may better accommodate its bird species' elevational range shifts, which are occurring due to various factors, including climate change (Maggini et al. 2011, Şekercioğlu et al. 2012), thereby maintaining greater compositional stability. Although the strength and direction of elevational shifts vary across species and regions, the phenomenon of European bird communities shifting their elevational ranges is well documented (e.g., Popy et al. 2010, Maggini et al. 2011, Bani et al. 2019, Hallman et al. 2022). These shifts appear to be driven by a combination of biotic and abiotic factors. Species expanding or contracting their elevational ranges may be tracking changes in their ecological niches or responding to shifts in ecosystem components, such as the distributions of other organisms (Ruiz-Labourdette et al. 2012, Vitasse et al. 2021). As a consequence, shifts in biotic and abiotic elements, including phenological changes, may be resulting in a shift of the whole niche availability zone. This mechanism may explain the positive association between mean elevation and functional stability: squares with high mean elevation and elevational variability may continue to provide stable ecological conditions by accommodating shifting elevational niches, thereby promoting functional stability in bird communities.

Second, reduced overall lower human impact at higher elevations may have contributed to higher stability of breeding bird communities in this study. Previous research has demonstrated that overall human impact tends to be lower at higher elevations (Brooks et al. 2002, Körner 2004). Unfortunately, a robust measure of human impact on nature, such as the Human Footprint Index (Sanderson et al. 2002), was not available for the study period. Additionally, variables that indirectly measure human impact, such as the land cover change variables, were eliminated early in the

model selection process (see section 2.4.2.3.5 for a discussion on this). However, when I manually included the land cover change variables to the final model, the significance of the mean elevation variable persisted. This led me to conclude that any stabilizing effect of higher mean elevation, other than offering a wider range of elevations, is likely mediated by lower human impact beyond just land cover change. Overall, I believe that the main mechanism through which higher mean elevation enhances community stability is by offering a wider elevational range, which facilitates species' elevational shifts and buffers against environmental changes.

2.4.2.3.3 Land surface area

Land area in study squares is another variable that was excluded during the model selection process due to collinearity. In particular, this variable was strongly and significantly correlated with both stabilizing dispersal potential indices. Since these indices were defined in a way that inherently incorporates an area effect (see section 2.2.9.2.9 for further details), I retained them in the models. My primary interest was to explore their effects on community stability rather than the well-established effects of area alone (MacArthur and Wilson 1967, Simberloff and Abele 1976, Whittaker and Fernandez-Palacios 2007). To disentangle the relative importance of these variables for taxonomic and functional stability, I employed variance partitioning (Paula-Souza and Diniz Filho 2020). I used the utilities of the *performance* package (Lüdecke et al. 2021) in R (R Core Team 2024) to calculate the unique variance explained by the taxonomic and functionally stabilizing dispersal potential and land area. Bootstrapping was used to estimate 95% confidence intervals and to test whether the contributions differed significantly. The unique variance explained by the taxonomically stabilizing dispersal potential index was 17.6% (95% CI: 15.2-19.0%), and it was significantly higher than that of land area, which accounted for only 1.2% (95% CI: 0.3-2.1%). The unique variance explained by the functionally stabilizing dispersal index was lower, yet significant 12.4% (95% CI: 9.5-15.3%). Once again, the unique contribution of the land area

was minor 1.7% (95% CI: 0.3-3.1%) and significantly lower than that of the dispersal potential index. Given these results, I removed land area from the models and proceeded the analyses with the stabilizing dispersal potential indices.

2.4.2.3.4 Proportion of protected areas

The results of the analyses showed that the proportion of protected areas within study squares was positively associated with the compositional stability of their breeding bird communities (Figure 2.26 in section 2.3.2.1). However, unexpectedly, a similar relationship between functional stability and protected areas was not observed in this study.

Protected areas can be highly effective at mitigating human-caused disturbances and habitat degradation, thereby better maintaining compositional stability of their communities compared to non-protected areas (Geldmann et al. 2014, 2019). By limiting disturbances such as urbanization, deforestation, and agricultural expansion, protected areas can reduce turnover in species composition and help maintain stable community compositions (Gray et al. 2016). Additionally, some protected areas implement targeted conservation measures for certain species through habitat management and direct intervention for species protection (Hodgson et al. 2011). These factors may explain the positive relationship between the proportion of protected areas in a square and taxonomic stability of its bird communities. However, this positive impact may not necessarily translate to functional stability, as functional stability is influenced by more complex ecological processes, such functional redundancy, positioning of species in functional space with respect to others in the greater species pool, and environmental filtering (Mason et al. 2005b, Biggs et al. 2020). Functional stability of ecological communities is expected to depend on species' traits, their redundancy, and their capacity to buffer environmental fluctuations (Elmqvist et al. 2003, Laliberté et al. 2010). In particular, functional redundancy, which is a key determinant of functional stability (Mori et al. 2013, Biggs et al. 2020), is not necessarily higher in protected areas. This suggests that

protected areas may not be inherently better at maintaining its communities' functional stability compared to non-protected areas. Additionally, because of the method used to define functional stability in this chapter (section 2.2.8), species additions can also reduce functional stability. In this case, the magnitude of change in functional volume occupied depends on the exact positioning of the species in functional space with respect to the entire species pool, and the functional positioning of the colonizing species. For example, if a colonizing species is functionally distinct from the existing community, it may introduce substantial changes in functional composition, regardless of whether the site is protected or not. This may explain the lack of a positive relationship between functional stability and protected areas. See section 2.4.2.2 for a more thorough discussion on how functional properties of communities can influence their functional stability.

2.4.2.3.5 Land cover change

Previous studies conducted in Europe have demonstrated that land cover change plays a major role in shaping breeding bird distributions in the region (e.g., Soultan et al. 2022, Howard et al. 2023). Therefore, I expected to observe a negative impact of land cover change on community stability in this study. However, none of the selected models included any land cover change variables. These unexpected results may be attributed to several of factors.

First, the dataset used to assess land cover changes was ESA's CCI Global Land Cover product (ESA-CCI-LC; CCI 2017), which does not fully encompass the time period between the two atlases. The earliest available data in ESA-CCI-LC is from 1992, meaning it fails to capture the initial land cover for most of the study squares. As a result, the two methods I used to quantify land cover change, the number of pixels changed and the Bray-Curtis dissimilarity (section 2.2.9.2.5), may not reflect the true nature of the land cover changes due to this missing time interval for many study squares. However, given its temporal and spatial coverage, this dataset was the best available alternative, so I proceeded with its use while acknowledging this

limitation. This issue would be less concerning if land cover change rates across the study region were equal or comparable, an assumption I made for the covered and missing time intervals (section 2.2.9.2.5). However, due to the lack of data, it is impossible to verify whether this assumption holds or not.

Second, the 37 land cover classes that the dataset offers were classified into nine broader IPCC categories (see Table 2.7 in section 2.2.9.2.5), which did not yield significant associations with stability. A different land cover classification may better capture habitat changes. Unfortunately, to the best of my knowledge, an alternative classification that is ecologically more meaningful for studying bird communities is currently not available, and simply aggregating the classes given in the ESA-CCI-LC dataset may not be optimal, as it would introduce additional subjectivity. Third, the two land cover change quantification methods employed in this chapter may not have been the most optimal approaches for capturing ecologically relevant changes. In this study I employed two quantification methods reflecting two different approaches. The Bray-Curtis dissimilarity approach that I used (section 2.2.9.2.5) compares the “before” and “after” states of the squares to calculate a dissimilarity metric based on land cover pixels. This implies that, the metric calculated here is completely insensitive to the spatial arrangement of the pixels, as it solely relies on relative “abundances” of the land cover classes. The “number of pixels changed” approach is expected to capture such changes, but it may not have detected ecologically meaningful shifts as it does not consider the identity of the classes.

Third, land cover changes in the study area over the study period were rather limited in extent. Overall, the median percentage of pixels that changed to any other class were only 7%, and 90% of the squares experienced land cover changes in less than 17% of their total area (Figure 2.30).

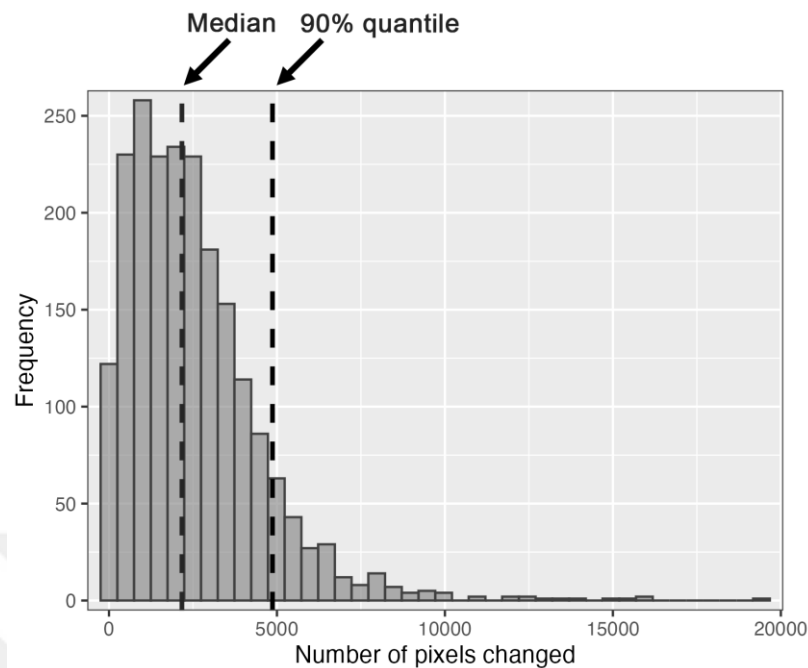


Figure 2.30 Histogram of number of pixels changed for the study squares over the study period. Dashed lines show the median (left) and 90% quantile threshold (right).

Such small-scale changes in land cover might not have been strong enough to cause range shifts or extinctions in squares that were 50 km x 50 km in size. This may have contributed to the lack of a significant relationship between land cover change and community stability.

Fourth, some potentially influential factors, such as land-use intensity, pollution, or hunting, may not be reflected in land cover classification alone. For instance, land cover change analyses relying solely on classification would fail to capture changes in a cultivated land patch where non-irrigated agriculture has persisted for four decades while pesticide use has steadily increased. Despite the lack of visible land cover change, this increasing pesticide input could have detrimental consequences for bird communities (Chiron et al. 2014). Similar analogies can be suggested for the amount lumber harvested from a forest or plant biomass removed from a pasture (Kuemmerle et al. 2016). Similar examples include the amount of lumber harvested from forests or plant biomass removed from pastures (Kuemmerle et al. 2016).

Unfortunately, I did not have access to such data, and the land cover analyses conducted here fail to capture these changes. Incorporating land-use information into future analyses could reveal stronger relationships with community changes.

Lastly, the spatial scale of the analysis may not have been optimal for detecting the effects of land cover change on bird communities. Previous research has demonstrated that the responses of bird communities to land cover change can vary across spatial scales (Allen et al. 2019, Frishkoff and Karp 2019; also see Chapter 1 of this thesis). The ESA-CCI-LC dataset has a spatial resolution of 300 m (CCI 2017), and I used this native resolution for measuring the land cover change. However, land cover changes at such fine scales may not strongly influence bird communities measured at 50 km x 50 km scale, as birds have extraordinary movement capabilities and may respond more to land cover changes at broader spatial scales (Lovette and Fitzpatrick 2016, Fusco et al. 2021). To explore this, I conducted a small trial by aggregating the land cover data by a factor of four, effectively decreasing the spatial resolution to approximately 1.2 km. Unfortunately, even at this coarser resolution, the effect of the land cover change variables on community stability were statistically insignificant. Alternatively, although not available for this study, bird data collected at finer spatial resolution could also provide the same effect. Considering these points, I recommend that future studies to try and find a dataset with full temporal coverage of the study period, define and apply ecologically more meaningful land cover classifications, test a wider range of metrics to measure land cover diversity, and consider conducting analyses at larger spatial scales to better capture bird community responses to habitat changes.

2.4.2.3.6 Initial land cover diversity

Contrary to my expectation that there would be weak but positive effect of initial land cover diversity on community stability (section 2.1.3.3), initial land cover diversity did not have any significant influence on the taxonomic and functional stability of the breeding bird communities over the study period. This may be

because, as I had suspected, the nature of land cover changes that occur, rather than initial land cover diversity, may be a stronger potential determinant of community stability. This finding contradicts the results of my oversimplified simulations (section 2.1.3.3), which may have been too simplistic to capture the real-world changes. Additionally, initial data exploration suggested that there may be a unimodal relationship between initial land cover diversity and community stability. However, since the modeling approach used in this chapter, the spatial error models (SEMs; Anselin 1988, Bivand 2008), does not allow for smooth terms, I was unable to model this variable using a smoother. Future studies employing alternative modeling approaches, such as generalized additive models (GAMs; Wood 2017), could provide a deeper insight into this relationship.

2.4.2.3.7 Climate change

Previous research has shown that changes in temperature and precipitation can influence bird distributions, although the strength and direction of these effects largely depend on the species, habitat, and season under consideration (Sillett et al. 2000, Reif et al. 2010, Iknayan and Beissinger 2018, Fogarty et al. 2020). Since this study includes a total of 389 species with diverse ecological requirements and habitat preferences (see Appendix B.1 for a full list of study species), formulating specific hypotheses regarding the effects of changes in temperature and precipitation was challenging. Nevertheless, I proceeded with the hypothesis that climate variables examined in this study would have a negative effect on community stability. Among the tested six variables of climatic change, only change in temperature of the warmest quarter and change in annual temperature and precipitation, both in terms of directionless magnitude, were retained in the final models after the model selection process. The model results showed that changes in temperature of the warmest quarter were negatively associated with taxonomic stability, as I had hypothesized (Figure 2.26 in section 2.3.2.1). However, unexpectedly, changes in annual

temperature and precipitation variable were positively related to the functional stability of the study communities (Figure 2.28 in section 2.3.2.2).

Temperature can manifest its impact on bird communities by influencing thermoregulatory and metabolic costs (Conradie et al. 2023), causing direct mortality (Schaefer et al. 2008), imposing higher fitness costs due to phenological shifts (Taff and Shipley 2023), altering overall habitat suitability (Mota et al. 2022), modifying species interactions (Martin and Maron 2012) such as altering the disease or parasite loads (Mennerat et al. 2021). A combination of these mechanisms may explain why communities experiencing greater changes in temperature during the warmest quarter, which largely coincides with summer in the study area, exhibited greater changes in their taxonomic composition. This finding also aligns with findings of previous studies that reported range shifts in birds due to climate change (Thomas and Lennon 1999, Huntley et al. 2006, Jiguet et al. 2006, Murphy and Romanuk 2014, Gillings et al. 2015, Currie and Venne 2017, Howard et al. 2023).

The two-dimensional change in annual temperature and precipitation was found to be positively related to functional stability in this study, which contradicted my expectation. There may be several reasons behind these observations. First, the influence of changing climate on birds may not as strong as I thought it would be. In other words, changes in temperature and precipitation may not have had a significant effect on community stability, and thus, the analyses failed to detect any meaningful associations. This possibility is supported by previous studies that reported weak effects of climate on bird distributions (e.g., Saultan et al. 2022, Howard et al. 2023). Second, the method I used to quantify these 2D climate change measures may not have been the most optimal way to measure climate change. In this approach, temperature and precipitation variables are first standardized and placed on axes, and then the absolute shift between time periods was calculated as the Euclidean distance (Figure 2.19 in section 2.2.9.2.7). Here, the two variables are given equal weight, suggesting that temperature and precipitation contribute equally to climate-driven changes. This may not be the case in reality, where either one of the temperature or precipitation changes can be more influential than the other (Fogarty et al. 2020).

This implies that testing different weights could have yielded different results, although the high diversity of habitats and species included can still introduce a “cancelling out” effect, masking any significant, directional associations. Third, by focusing solely on mean temperature and precipitation-based variables, I may have overlooked other potentially influential aspects of climate, such as seasonality, variability or the frequency and intensity of extreme climatic events (Williams and Middleton 2008, Fick and Hijmans 2017, Wingfield et al. 2017). While temperature and precipitation are important components of climate, they may not always be the most influential aspects of climate, through which climate change impacts community stability. For instance, extreme weather events experienced during winter or breeding season can have detrimental consequences for various breeding bird species (Pipoly et al. 2013, Cohen et al. 2021). Fourth, the model selection strategy I used, namely backward selection, may have played a limiting role in this analyses. Since I accounted for differences in EBBA1 and EBBA2 survey dates across study squares and adopted a time-sensitive approach, the quantified climatic variables inherently included a time effect (section 2.2.9.2.7). This means that, the ideal way to test the effect of these variables would have been to do so in the presence of another variable in the same model that carries information about the time gap between the EBBA1 and EBBA2 surveys. Unfortunately, neither of the two selected models included this time gap variable. This is an inherent limitation of the backward selection method, as it prioritizes statistical significance over variable importance (Burnham and Anderson 2002, Harrell 2015). To further investigate this issue, I manually included the time gap variable in the selected functional stability model that originally contained the 2D annual temperature and precipitation change variable. Just as I expected, caused the previously significant positive effect of annual temperature and precipitation change on community stability (estimate: 0.002, SE: 0.001, p-value = 0.01*) on community stability (see Figure 2.28 in section 2.3.2.2) to lose statistical significance (estimate: 0.001, SE: 0.001, p = 0.21). This suggests that observed positive effect of the 2D annual temperature and precipitation change may, at least partially, be an artifact of the dataset structure and model

selection method used. Tailored models that include both climate-related and time gap variables could provide deeper insights into this issue. However, I will refrain from such an approach, as it would constitute an extreme case of statistical “phishing” and my models are not intended for predictive purposes (Burnham and Anderson 2002, Whittingham et al. 2006). To have a deeper insight into the potential underlying mechanisms for this unexpected positive relationship, I manually included the interaction of mean annual temperature and total annual precipitation, the BIO1 and BIO12 variables from the BioClim dataset, respectively (Fick and Hijmans 2017), in the global model and repeated the model selection procedure (section 2.2.10.2). Being directionless, the 2D climate change variable I used here (section 2.2.9.2.7) would be unable to distinguish between a case with increases and decreases in both variables, as it focuses on absolute changes, further justifying this extra analysis. To my surprise, this interaction term was included in the final model and had a significant positive effect size estimate (estimate: 0.0011, SE: 0.0004, $p = 0.0187^*$). This positive interaction effect between standardized annual precipitation (BIO12) and mean annual temperature (BIO1) on the functional stability of breeding bird communities suggests that the combined increase of both factors enhances community stability more than either factor, both of which had statistically insignificant effects in the models. These findings suggest the observed positive effect between the 2D annual temperature and precipitation change variable and functional stability may be due to the increased stability in areas that had increased annual precipitation and temperature. Such warmer temperatures coupled with increased precipitation can lead to more robust primary productivity, providing abundant food resources for breeding birds (Gorzo et al. 2016, Catano et al. 2020). This abundance may, in turn, can support stable communities.

The lack of significant effects from individual temperature or precipitation variables on community stability may be due to the vast geographic scope of this study, which encompasses a wide range of habitats and species with varying sensitivities to climatic changes. It is known that responses to changes in temperature and precipitation vary across habitat and bird taxa considered (Sillett et al. 2000, Iknayan

and Beissinger 2018, Fogarty et al. 2020). In addition, the opposing responses to these climatic variables may have cancelled each other out in analyses. For example, a habitat-modifying drought risk as a response to increase in temperature may be cancelled out by an increase in precipitation. Lastly, the lack of significant relationships can also be attributed to extinction debts. Extinction debts are the delayed extinction of species following environmental changes, such as habitat destruction or climate change (Kuussaari et al. 2009). According to this idea, even if suitable habitats are reduced or degraded, some species' existence may persist temporarily due to lag effects, but they are doomed to disappear eventually if conditions do not improve. In such cases declines in abundance precede complete losses of species (Böhning-Gaese and Bauer 1996, Parody et al. 2001, Şekercioğlu et al. 2004, Rosenberg et al. 2019), and since the data available for this study is in the form of incidence data, such changes may have gone undetected in this study. This may as well be what happened to the study communities over study period, which is supported by findings of a study that used the same dataset suggested that the species in the region could actually be in a climatic debt (Howard et al. 2023).

2.4.2.3.8 Biomes

My hypotheses regarding the effect of biome coverage on community stability predicted negative relationships between the coverage of grassland and Mediterranean biomes (section 2.2.9.2.8) and community stability, as these biomes are experiencing elevated levels of human impact and climate change vulnerability (Cremene et al., 2005; Habel et al., 2013; Sala et al., 2000; Török et al., 2017; Underwood et al., 2009). However, the results of the analyses showed that the Mediterranean and tundra biomes were the ones associated with lower levels of taxonomic stability, while the temperate conifer forest biome was positively related to both taxonomic and functional stability (Figures 2.26 and 2.28 in section 2.3.2).

The lower compositional stability of breeding birds in the Mediterranean forests, woodland, and scrub biome can be attributed to a combination of factors. First,

human impact is relatively high in this biome. The Mediterranean basin is one of the most densely populated regions in Europe, and deforestation, urbanization, and agricultural intensification continues to degrade natural habitats (Brotons et al. 2004, Sirami et al. 2008, Kuemmerle et al. 2016). The expansion of intensive farming and monocultures has particularly contributed to habitat fragmentation and biodiversity loss in the region (Ellis et al. 2010, Sokos et al. 2013). Second, the Mediterranean basin has experienced some of the most rapid trends of warming over the past few decades. Summers have become hotter, drier, and longer due to climate change (Giorgi and Lionello 2008). Climate change and human activities have also increased the wildfire frequency and intensity in the region, with severe consequences for bird communities that depend on woodland and shrub habitats (Pausas and Keeley 2019). Third, uncontrolled surface and ground water extraction for irrigation, tourism, and domestic lead to degradation of wetlands and riparian habitats in the region, threatening birds depending on these habitats (Green et al. 2017, Yılmaz et al. 2021, Çolak et al. 2022). Fourth, the Mediterranean region constitute the warmest edge of distributional ranges of many species, and a quick look at the distributions of some of the breeding bird species in Europe confirms that (Keller et al. 2020). Previous studies suggest that local extinctions are common in warmer edges of distributional ranges of animals, including birds (Wiens 2016). If that is the case in the study area, then species located in the warm Mediterranean may already be living at the edge of their ecological tolerance limits, making extinctions more likely here due to environmental changes such as climate change. In my view, the Mediterranean biome may be experiencing more extinctions due to these reduced dispersal opportunities. Lastly, the Mediterranean basin, especially Southern Europe, is a hotspot for bird trapping and hunting, causing direct mortality of hundreds of thousands of birds each year (Brochet et al. 2016). All of these factors may have influenced bird phenology, resource availability, and breeding success, ultimately leading to higher species turnover and lower compositional stability in this biome.

The tundra biome exhibited higher compositional change in its breeding bird communities, likely due to a combination of environmental and anthropogenic

factors. First, the Arctic and tundra regions are warming twice as fast as the global average (Post et al. 2019). Rising temperatures alter the timing of snowmelt, accelerate permafrost thawing, and drive vegetation shifts, disrupting breeding phenology and resource availability for birds breeding in the region (Høye et al. 2007). Changes in habitat structure may also favor shrub expansion, modifying nesting conditions and food availability for tundra-dependent bird species (Boelman et al. 2015, Flemming et al. 2019). Second, most of tundra-breeding birds are long-distant migrants birds, making them particularly vulnerable to multiple stressors across their annual cycle. These include phenological mismatches bird arrival and peak food availability at both breeding and wintering grounds, as well as deterioration of conditions at wintering grounds and stopover sites (Skagen 2006, Clausen and Clausen 2013, van Gils et al. 2016). Migration-related pressures can affect survival rates, reproductive success, and population dynamics, ultimately leading to higher compositional changes (Sanderson et al. 2006). Third, the human disturbance in the tundra has been increasing, further pressuring this fragile biome. Resource extraction activities such as oil drilling, mining, and infrastructure development in the Arctic are altering tundra-breeding birds' habitats (Rozell et al. 2024). Additionally, the expansion of Arctic shipping routes due to melting sea ice may also introduce pollution, invasive species, and novel predators to already sensitive tundra ecosystems (Meltotte 2018). Fourth, as I mentioned in the preceding paragraph, the reduced dispersal opportunities in the tundra biome may have resulted in species extinctions in this biome. This is because, the tundra biome constitutes the northernmost part of the study area, suggesting that the species inhabiting this biome may face higher extinction rates because they have nowhere else to shift their ranges to (Thomas et al. 2004, Parmesan 2006). A quick look at the species richness difference map confirmed this: the squares located within the tundra biome seem to have experienced a decline in their species richness (Figure 2.31). Lastly, rapidly increasing temperatures and changing habitat structure have been facilitating range shifts in generalist predators, such the red foxes (*Vulpes vulpes*), which are expanding into the tundra (Fuglei and Ims 2008). Colonization of the tundra by more

generalist predators (e.g., foxes, gulls, ravens) has increased predation pressure on tundra-breeding birds, leading to higher nest failure rates (McKinnon et al. 2010). Given these combined factors, it is unsurprising that the tundra biome exhibited lower breeding bird community stability over the study period, as all of these factors have the potential to reshape the communities. I would expect all of these changes to cause species extinctions

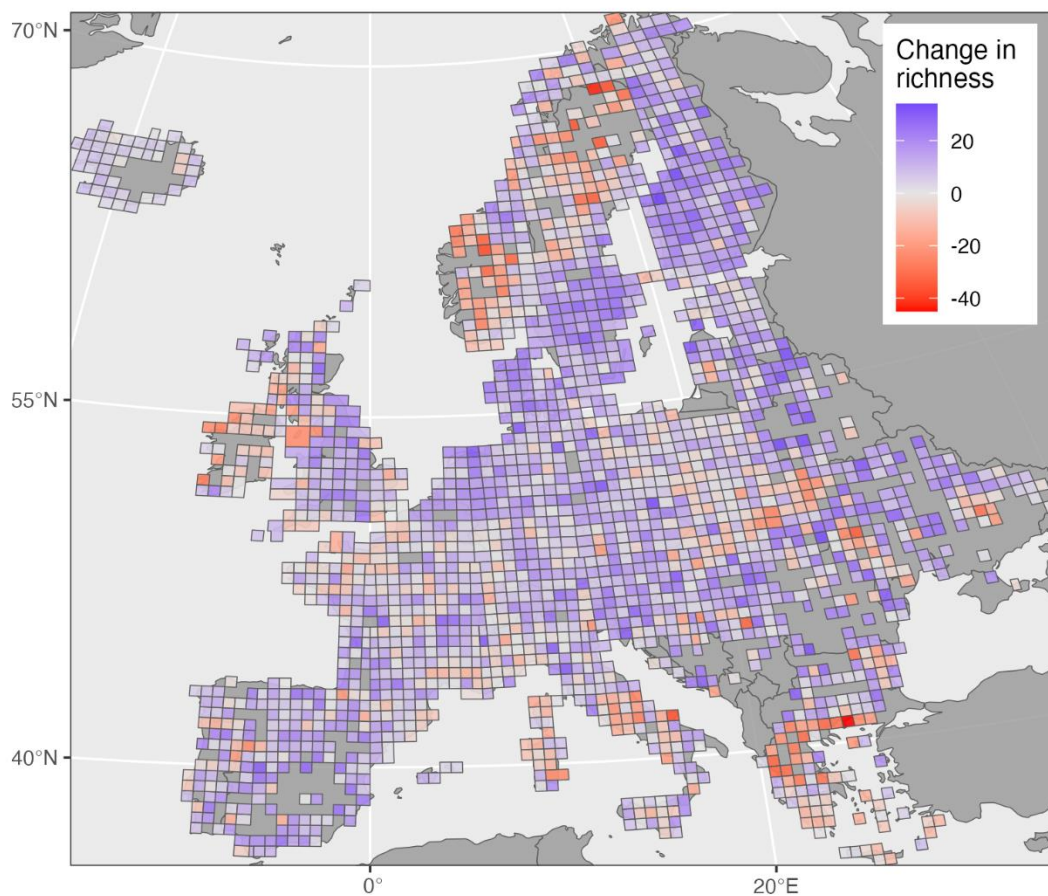


Figure 2.31 Net change in species richness for the study squares over the study period.

The lack of significant relationships between the Mediterranean and tundra biome coverage and functional stability can be attributed to the fact that functional stability of the communities may depend on more complex ecological processes, such as the dominant community assembly rules (Nemergut et al. 2013), and intrinsic properties

of communities such as functional redundancy of the species (Mori et al. 2013, Biggs et al. 2020).

The temperate conifer forest biome was the only biome that positively impacted both taxonomic and functional stability of the study communities. Although I had no particular hypothesis regarding this biome, several factors may explain these positive relationships. First, conifer forests in Europe are well maintained and protected. Sustainable forest management practices, including selective logging, controlled burns, and continuous cover forestry, have likely helped maintain habitat structure and support bird populations inhabiting these habitats (Barbati et al. 2007, Adámek et al. 2015, Lier et al. 2022). These management strategies can reduce habitat degradation while promoting biodiversity by ensuring the presence of mature trees, standing deadwood, and diverse undergrowth, all of which are essential for forest-dwelling birds (Lindenmayer and Laurance 2017, Arcilla and Strazds 2023). Second, temperate conifer forests in Europe have experienced relatively lower levels of land-use change over the past decades. Conservation policies have restricted large-scale deforestation and promoted afforestation, which may helped maintain stable bird communities in these habitats (Leitão et al. 2022). Lastly, the limited expansion of urban areas in conifer-dominated habitats has helped maintain large tracts of continuous forest, possibly benefitting forest-dependent bird species (Spiecker 2003, Santini et al. 2016). Compared to other biomes, anthropogenic pressures such as agricultural expansion and urbanization have been relatively less intense in temperate conifer forests of Europe (Kuennecke 2008, Ellis et al. 2010). The persistence of large, connected forest patches ensures the continued presence of specialist species (Betts et al. 2019). Because of the factors listed here, including the effective conservation policies and lower land-use pressures, breeding bird communities in temperate conifer forests may have remained taxonomically and functionally stable over the study period. However, given the alarming decline of resilience of these ecosystems to withstand perturbations, the enhanced bird community stability observed within the temperate conifer forests for the period between EBBA1 and EBBA2 may disappear in the near future (Forzieri et al. 2022).

2.4.2.3.9 Stabilizing dispersal potential

Dispersal is a critical process that can mitigate local extinctions by enabling recolonization and keeping population sizes at viable levels (Hanski 1998, Eriksson et al. 2014). Thus, dispersal dynamics has the potential to enhance taxonomic and functional stability of local communities (Weiher and Keddy 2001, Leibold et al. 2004, Scheiner and Willig 2011). In this study, taxonomically and functionally stabilizing dispersal potential indices (section 2.2.9.2.9) were found to be positively related to the taxonomic and functional stability of breeding bird communities (Figures 2.26 and 2.28 in section 2.3.2). This findings confirmed my hypotheses, and in this section, I will discuss possible underlying mechanisms for these positive relationships.

Immigration of individuals from other populations in a metapopulation can reduce the probability of local extinctions by boosting local population sizes, thereby buffering them against demographic or environmental stochasticity (Brown and Kodric-Brown 1977, Eriksson et al. 2014). This reduction in local extinction probability, known as the rescue effect (Brown and Kodric-Brown 1977), can play a crucial role in maintaining the viability of local populations and even the entire metapopulation (Hanski 1998, Eriksson et al. 2014). Previous research has demonstrated the importance of rescue effect across various taxa, including birds (Hanski 1998, Pavlacky et al. 2012, Dornier and Cheptou 2012, Van Schmidt and Beissinger 2020). The rescue effect may partially explain why squares that initially had taxonomically or functionally similar neighbors stayed more stable over the study period. Such squares likely received immigrants from their neighbors, enhancing viability and stability of their bird communities. Similarly, in the case of new colonizations or range expansions, communities that were surrounded by taxonomically or functionally similar squares had a higher probability of receiving species already present in the community (due to the high taxonomic similarity with the neighbors). Even if the colonizing species was new to the square, it would likely have functional traits similar to the ones in the destination community (due to the

high functional similarity with the neighbors). The mechanisms outlined here can explain the positive relationship between the dispersal potential indices and community stability, which are somehow in line with findings of previous studies that reported realized occupancy in breeding birds was strongly influenced by distance to the nearest occupied square over the same study period (Howard et al. 2023). However, I believe that an improved dispersal potential index that accounts for the distance-dependent and species-specific nature of the dispersal, as well as the geography-imposed costs of dispersal (Paradis et al. 1998, Sutherland et al. 2000, Garcia-R and Matzke 2021), could reveal even stronger associations with community stability. Future studies should consider exploring such complex stabilizing dispersal potential indices.

2.4.3 Quantification of community stability

Stability is a multifaceted concept, and quantifying of the multiple aspects of it is recommended for a complete understanding of changes in ecological systems (McCann 2000, Ives and Carpenter 2007, Donohue et al. 2013). However, most studies focus on a single component, stability (Donohue et al. 2016). In this chapter, I quantified community stability using a single component, resistance, measured through temporal beta diversity (section 2.2.8). This means that, like other studies that employ a single stability metric, this study risks underestimating potential effects of perturbations on stability of ecological communities (Donohue et al. 2016).

The use of the resistance component as a measure of stability in this chapter is further justified by the fact that studies focusing on the resistance component should primarily consider press disturbances, which are long-term, chronic stressors that continuously impact a system, such as climate change and habitat degradation (Smith et al. 2009, Shade et al. 2012). Because resistance measures how well a system can withstand change (Johnson et al. 1996, McCann 2000), it is best suited for evaluating responses to press disturbances, where the system experiences sustained stress over time. Although resistance can also be used to study the impact of pulse

disturbances—short-term, discrete events such as storms, wildfires, or temporary droughts (Grimm and Wissel 1997), the resilience component is often more appropriate for assessing recovery from these types of changes. Resilience would not be a suitable measure for evaluating the outcomes of the persistent environmental changes investigated in this chapter due to the absence of a predefined baseline and the unavailability of data at more than two points in time.

Another potential limitation of the approach employed in this chapter concerns the calculation of functional stability. I measured functional stability using functional beta diversity, which relies on quantification of convex hull volumes functional space (Villéger et al. 2011). In this method, the most convex hypervolumes for each community are computed, and beta diversity indices are derived from the overlapping and non-overlapping volumes (see section 2.2.8; Magurran and McGill 2011, Villéger et al. 2011). However, convex hulls have an inherent limitation: they are insensitive to the presence or absence of species with intermediate trait values (Cornwell et al. 2006, Villéger et al. 2008a). This means that if a species has intermediate trait values, its addition or loss will not alter the convex hull and thus, the subsequent functional beta diversity calculations.

Although computationally more demanding, alternative methods, such as using n -dimensional hypervolumes based on kernel density functions (Legras et al. 2018, Mammola and Cardoso 2020, Latombe et al. 2024), can potentially overcome this weakness. Nevertheless, most studies examining functional stability focus only on a single function (see section 2.1.1). Compared to these studies, using convex-hull-based functional beta diversity, calculated with multiple traits, offers some advantages such as representing multiple niche dimensions. Therefore, when dealing with large datasets, like the examined in this chapter, using convex-hull-based hypervolumes can be a reliable alternative to kernel-density-based hypervolumes potentially superior yet computationally more demanding approaches such as the ones that rely on kernel-density-based hypervolumes, which, while potentially superior, are significantly more computationally intensive.

It should be noted that kernel-density-based hypervolumes have their own methodological drawbacks too, such as the dependence of results on grid size selection in density function calculations (Mammola and Cardoso 2020, Carmona et al. 2024, Latombe et al. 2024). However, I strongly recommend that future studies consider employing the kernel-density-based hypervolumes approaches in functional stability calculations for studying functional stability of communities if the dataset size allows for it.

2.4.4 Future recommendations

I recommend future studies focusing on taxonomic and functional stability of breeding bird communities using the same breeding bird atlas datasets (EBBA1 and EBBA2 (Hagemeijer and Blair 1997, Keller et al. 2020) consider using alternative modeling approaches, different methods for quantifying temporal taxonomic and functional stability, and the development of predictive models to identify regions most vulnerable to taxonomic or functional changes in the future.

CHAPTER 3

CONCLUSION

In this thesis, I investigated spatiotemporal changes in bird communities at regional and continental scales. The first chapter focused on changes in diversity of breeding wetland bird communities across spatial scales in Konya Closed Basin, Türkiye, while the second chapter examined the intrinsic and extrinsic drivers of community stability in breeding bird communities across Europe.

The results of the first chapter revealed that wetland bird communities in the Konya Closed Basin became more heterogeneous due to species losses, with functional diversity declining far more than taxonomic diversity at the regional scale. The results of the second chapter showed that the temporal stability of the communities was linked to various extrinsic factors like mean elevation, biome coverage, climate change, and whether the local patches were surrounded by taxonomically or functionally similar patches. Overall, the findings supported the diversity-stability hypothesis (MacArthur 1955), showing that communities with higher diversity tended to remain more stable over time.

In the Konya Closed Basin, taxonomic diversity declined by 19%, while functional diversity declined by 66% over a 20-year period (Section 1.3) in Konya Closed Basin, Türkiye over the course of 20 years. In contrast, European bird communities remained relatively stable over a 30-year period, with a mean taxonomic and functional stability value of 0.88 (Section 2.3.2). This discrepancy is likely due to differences in protection measures and conservation policies. Wetlands in Konya Closed Basin in Türkiye have been heavily degraded and drained over the past two decades (Yılmaz et al. 2021). Uncontrolled surface and groundwater abstraction has caused groundwater levels to drop by an average of 1.5 meters per decade, leading to the disappearance of marshes that were as large as entire districts (Eken et al. 2006,

Yılmaz et al. 2021). The degradation is ongoing, with Important Bird Areas (IBAs), such as Lake Kulu, have been completely drained (Özgencil and Uslu 2021). In contrast, effective conservation laws and enforcement in Europe have apparently contributed to greater stability in bird communities (Acreman et al. 2007, Keulartz 2009, Hoffmann et al. 2018). This may partially be because of the fact that habitat degradation and land use changes peaked before the study period in Europe (Kuemmerle et al. 2016), and despite the longer study duration (30 years versus 20 years), the land cover changes were mostly minor in Europe, unlike in Konya Closed Basin (Yılmaz et al. 2021).

The observed differences between Türkiye and Europe suggest that habitat protection and restoration are critical for preventing further biodiversity loss in Konya Closed Basin. Given the widespread habitat degradation in the Konya Closed Basin, these patterns are unlikely to be unique to wetland birds, and similar declines are expected for other bird groups (Eken et al. 2006, Yılmaz et al. 2021). Protecting the remaining wetland bird diversity will require large-scale conservation measures, including policy changes to regulate water use and strict limitations on groundwater and surface water abstraction. Once these foundational policies are in place, restoration efforts should focus on rehabilitating lost wetlands, ensuring they provide sufficient water levels and that islands remain intact during the breeding season to support nesting birds.

Although the situation in Europe is more optimistic, some regions, such as the Mediterranean and tundra biomes are experiencing declines in their bird diversity. Unfortunately, human impact and global climate change is transforming these biomes and damaging its bird communities. Protecting these communities will require both mitigating global climate change and curbing further habitat destruction caused by human activities. While bird communities in higher elevations appear to be doing better, their survival is also under threat. Climate change and human pressure are expected to push these communities to even higher elevations until no further refuge remains, leading to extinctions, increasing isolation between habitat patches, and further reduced dispersal potential (Thomas et al. 2004, Parmesan

2006). This study also demonstrated that, although through different mechanisms, climate change exerts a negative impact on bird communities in both study areas, further highlighting the importance of addressing this human-caused crisis.

The results of the second chapter, which focused on the community stability of breeding bird communities in Europe, demonstrated that protected areas provided a certain degree of protection against changes in the taxonomic composition of these communities. Although the overall effectiveness of protected areas at resisting anthropogenic pressures can be questioned (Geldmann et al. 2019), nearly all types of protected areas impose some level of restriction on human activities and thus offer a degree of protection (Gray et al. 2016, Hoffmann et al. 2018). Given the ongoing biodiversity crisis and importance of birds as key ecosystem components (Şekercioğlu et al. 2016, Cowie et al. 2022), policymakers should consider both expanding protected area networks and ensuring their effective management in both Europe and Türkiye to better preserve bird diversity.

This study demonstrated that diversity can provide some degree of protection against shifts in communities' taxonomic and functional composition (Section 2.4.2). A detailed examination of the relationship between diversity and stability reveals that this relationship is complex, with certain components of functional diversity interacting in ways that either amplify or mitigate their impact on stability (Section 2.4.2.2.2). Future studies exploring interactions not examined here could provide further insight into how functional features influence community stability.

In this thesis, I utilized breeding bird atlases in both of the main chapters. Atlas studies serve countless important purposes in ornithological research, including assessing changes in distributions, population trends, understanding species-environment relations, identifying conservation priority areas, and predicting future changes in bird distributions (Donald and Fuller 1998, Brotons et al. 2007, Milanesi et al. 2017, Pototsky and Cresswell 2023). Today, atlas studies continue to be the standard method for mapping bird distributions and are among the most widely used data sources in avian research (Gibbons et al. 2007, Pototsky and Cresswell 2023).

For instance, the first European Breeding Bird Atlas (EBBA1), published in 1997 (Hagemeijer and Blair 1997), had been cited in 3,150 studies by 2018 (Herrando et al. 2019). Although atlas studies have been carried out in various parts of the world for decades (Gibbons et al. 2007, Pototsky and Cresswell 2023), there has been a notable lack of such efforts in Türkiye, with only a single country-level breeding bird atlas and a few local or regional atlases published to date (Boyla et al. 2019). Given their importance in providing large-scale and much-needed data on bird distributions and population trends, greater resources should be allocated to bird atlas studies in Türkiye. These future efforts should also consider incorporating abundance estimates or proxies, which would allow for a coarse yet valuable monitoring of bird population sizes.

The results from the two main chapters of this thesis also highlight the importance of considering multiple facets of biodiversity when investigating spatiotemporal responses of communities to environmental perturbations. It is well established that different aspects of biological diversity do not necessarily respond in the same way to environmental perturbations (Baraloto et al. 2012, Si et al. 2016, Bässler et al. 2016). Therefore, unless there is a specific question concerning a single facet of diversity a comprehensive understanding of ecological change requires the integration of multiple dimensions of biodiversity, such as taxonomic, functional, and even phylogenetic diversity.

Finally, given the ecological importance of birds (Şekercioğlu et al. 2016), future predictive studies that consider both extrinsic and intrinsic factors, and aim to identify the areas most vulnerable to taxonomic or functional diversity shifts are of utmost importance.

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APPENDICES

A. Appendix for Chapter 1

A.1 Lakes used in the remote sensing analyses

My colleague Mehmet Arda Çolak and I used satellite imagery for seven lakes, which are also important bird areas (IBAs), to assess the changes in the lake surface areas in different times of the year. Some fundamental information about these lakes is given below.

Lake Çöl

Lake Çöl (39°32' N, 32°86' E) is a shallow and brackish lake located at a mean elevation of 1,055-1,060 m (Eken et al. 2006). The lake had a surface area of 16.2 km² in spring 1996 (Yılmaz et al. 2021). The north of the area is covered mainly with agricultural lands, while there are wet meadows at the northern and southern ends of the lake (Kılıç and Eken 2004). In summer, the lake dries out to a great extent (Magnin and Yarar 1997). Agricultural intensification, unplanned construction, and illegal hunting are the most common threats in the area. When the water level was still high, the lake used to host breeding populations of Common Pochard (*Aythya ferina*) with up to 40 pairs and post-breeding populations of White-headed Duck (*Oxyura leucocephala*) with up to 13-14 pairs in the early 1990s (Yılmaz et al., 2021). The lake also used to hold up to 3,000 Common Pochards during their migration season (Yılmaz et al., 2021). In recent years, the water level has been very low, and almost all these species disappeared from the area.

Lake Tersakan

Lake Tersakan (38°58' N, 33°05' E) is a saline lake lying at 920-930 m above sea level (Eken et al., 2006). The surface area of the lake used to span nearly 52.8 km² in spring 1998 (Yılmaz et al., 2021). The lake used to have islands on which shorebirds, terns, gulls, and some ducks used to breed. The area surrounding Lake Tersakan is made up of saline meadows, steppes, and agricultural fields. The most severe threat for the lake is the drainage for agriculture use, which causes drying up of the lake (Eken et al., 2006). The marshes mentioned in some historical sources point out that the lake's water was less saline in the past (Yarar and Magnin, 1997).

Lake Uyuz

Lake Uyuz (39°24' N, 32°93' E) is a small freshwater lake with an altitude of 1,160-1,260 m (Eken et al., 2006). The surface area of the lake was only 0.31 km² in spring 1996 (Yılmaz et al., 2021). Surrounding dense reed beds that are found on the south and west coast of the lake have been home to breeding populations of the diving ducks such as White-headed Duck, up to 10 pairs of in 1994, and Common Pochard, up to 15 pairs, until the mid-2000s (Eken et al., 2006; Kılıç & Eken, 2004; Yılmaz et al., 2021).

Lake Samsam

Lake Samsam (39°06' N, 32°44' E) is a small and shallow freshwater lake that is fed by underground water, small streams, and precipitation (Kılıç and Eken, 2004). The lake is located at 980 m above sea level, and its surface area spanned almost 6.39 km² in 1998's spring (Kılıç and Eken, 2004; Yılmaz et al., 2021). The wetland is surrounded by steppes and agricultural fields, and the lake usually dries up at the end of summer (Kılıç and Eken, 2004; Yarar and Magnin, 1997). The salinity of the lake water decreased with the decreasing groundwater level of the lake, and vegetation formed. However, the soil around the lake remains saline, making it impossible to

use for agriculture (Yarar and Magnin, 1997). In the late-1990s, up to 30 pairs of White-headed ducks were found in the lake during the breeding season (Yılmaz et al., 2021).

Lake Bolluk

Lake Bolluk (38°44' N, 32°88' E) is a saline lake lied at a mean elevation of 940-990 m (Eken et al., 2006). The surface area of the lake was 9.34 km² in spring 1997 (Yılmaz et al., 2021). The IBA also includes the small shallow lakes to the south of the lake and the seasonal wet meadows and steppes between them (Kılıç and Eken, 2004). Due to the overall groundwater level fall in the northern part of Konya Closed Basin and the excessive water drainage for agricultural purposes, the lake has started to dry up in recent years (Eken et al., 2006). Islands in the lake used to support thousands of breeding waterbirds, including shorebirds, gulls, and terns.

Lake Kozanlı

Lake Kozanlı (39°01' N, 32°84' E) is a freshwater lake with an altitude of 980-1,030 m (Eken et al., 2006). The surface area of the lake used to span almost 1.18 km² in spring 1998 (Yılmaz et al., 2021). The area surrounding the lake consists of extensive wet meadows and marshes that are enclosed by farmlands (Eken et al., 2006). Lake Kozanlı used to host up to 10 breeding pairs of White-headed Duck and 15-20 pairs of Common Pochard until the mid-2000s (Yılmaz et al., 2021).

Lake Kulu (Düden)

Lake Kulu (39°08' N, 33°13' E) is a brackish and shallow found at 965-1,000 m above sea level. The lake had a total surface area of 12.28 km² in spring 1998 (Eken et al., 2006; Yılmaz et al., 2021). The lake consists of a small lake and a bigger one. Wet meadows surround the lake, and it used to have nine islands, some of which

contained important waterbird breeding colonies (Kılıç and Eken, 2004). Due to the declining water level, some of the islands and the mainland merged, which resulted in the collapse of the breeding waterbird colonies (Eken et al., 2006). Lake Kulu has been an important area for both breeding and migrating waterbirds. The lake is known as one of the most important former breeding sites of White-headed Ducks in Turkey (Eken et al., 2006; Yazar & Magnin 1997). In the early 2000s, up to 500 White-headed Ducks were molting in the lake (Yılmaz et al., 2021). Additionally, 30-40 pairs of Common Pochard and up to 30 pairs of White-headed Duck used to breed in Lake Kulu until the late-2000s (Yılmaz et al., 2021). Other duck species nest in the little lake located in the south of the area (Kılıç & Eken, 2004).

Imagery dates used in the remote sensing analyses and the surface areas that I obtained for each of the seven lakes are given in Table A.1.

Table A.1 Tables showing the imagery dates (DD.MM.YYYY; upper panel) and the lake surface areas obtained (km²; lower panel) for the seven lakes used in the remote sensing analyses (Lake Kulu is made up of two lakes: Kulu Big and Kulu Small).

Lake name↓ Date→	1996-1	1996-2	1997-1	1997-2	1998-1	1998-2	2016-1	2016-2	2017-1	2017-2	2018-1	2018-2
Kulu - big	7.05.1996	10.07.1996	1.05.1997	13.07.1997	11.04.1998	2.09.1998	28.04.2016	3.09.2016	15.04.2017	21.08.2017	4.05.2018	29.08.2018
Kulu - small	7.05.1996	10.07.1996	1.05.1997	30.08.1997	11.04.1998	2.09.1998	28.04.2016	3.09.2016	15.04.2017	21.08.2017	4.05.2018	29.08.2018
Uyuz	7.05.1996	10.07.1996	1.05.1997	30.08.1997	11.04.1998	2.09.1998	28.04.2016	18.08.2016	15.04.2017	21.08.2017	4.05.2018	29.08.2018
Çöl	7.05.1996	10.07.1996	1.05.1997	30.08.1997	11.04.1998	2.09.1998	14.05.2016	17.07.2016	15.04.2017	4.07.2017	4.05.2018	29.08.2018
Bolluk	7.05.1996	10.07.1996	1.05.1997	13.07.1997	11.04.1998	2.09.1998	28.04.2016	17.07.2016	15.04.2017	5.08.2018	4.05.2018	29.08.2018
Tersakan	7.05.1996	10.07.1996	1.05.1997	13.07.1997	11.04.1998	2.09.1998	28.04.2016	17.07.2016	15.04.2017	21.08.2017	4.05.2018	29.08.2018
Kozanlı	7.05.1996	10.07.1996	1.05.1997	30.08.1997	11.04.1998	2.09.1998	28.04.2016	18.08.2016	15.04.2017	21.08.2017	4.05.2018	29.08.2018
Samsam	7.05.1996	10.07.1996	1.05.1997	30.08.1997	11.04.1998	2.09.1998	14.05.2016	18.08.2016	15.04.2017	21.08.2017	4.05.2018	29.08.2018

Lake name↓ Area (km ²)→	1996-1	1996-2	1997-1	1997-2	1998-1	1998-2	2016-1	2016-2	2017-1	2017-2	2018-1	2018-2
Kulu - big	11.29	10.45	11.04	10.60	11.78	10.73	8.53	6.31	8.08	4.13	7.19	0.69
Kulu - small	0.50	0.43	0.47	0.43	0.50	0.46	0.40	0.36	0.39	0.33	0.38	0.30
Uyuz	0.31	0.23	0.23	0.17	0.23	0.14	0.22	0.12	0.19	0.11	0.18	0.10
Çöl	16.20	5.43	10.82	0.00	19.51	0.00	1.70	0.00	5.66	0.00	0.00	0.00
Bolluk	9.28	9.07	9.34	8.96	9.05	10.03	7.97	3.17	8.88	1.11	8.25	2.42
Tersakan	53.98	47.47	40.78	43.02	52.80	36.07	40.66	2.66	46.90	0.00	34.30	0.00
Kozanlı	1.11	0.90	0.44	0.52	1.18	0.46	1.47	0.78	1.38	0.84	1.30	0.81
Samsam	5.18	0.66	5.42	0.00	6.39	0.00	2.68	0.00	6.75	0.00	4.45	0.00

Whether a wetland bird will breed in a particular wetland or not can be influenced by the conditions of the previous years because (i) some important components of the wetland ecosystems such –as the extent of reeds and water level –will depend on

the preceding years' conditions (Moss 2013) and (ii) some of our study species reach sexual maturity at an age >1 (see S2). This is why we included a two-year period prior to 1998 and 2018 in our remote sensing estimates.

A.2 Species list

The full list of species that were included in the study is given in the table below.

Table A.2 List of the wetland bird species included in the study.

<i>Accipiter brevipes</i>	<i>Buteo buteo</i>
<i>Acrocephalus arundinaceus</i>	<i>Carduelis carduelis</i>
<i>Acrocephalus melanopogon</i>	<i>Cecropis daurica</i>
<i>Acrocephalus palustris</i>	<i>Cercotrichas galactotes</i>
<i>Acrocephalus schoenobaenus</i>	<i>Cettia cetti</i>
<i>Acrocephalus scirpaceus</i>	<i>Charadrius alexandrinus</i>
<i>Actitis hypoleucos</i>	<i>Charadrius dubius</i>
<i>Aegithalos caudatus</i>	<i>Charadrius leschenaultii</i>
<i>Alauda arvensis</i>	<i>Chlidonias hybrida</i>
<i>Alcedo atthis</i>	<i>Chlidonias leucopterus</i>
<i>Anas acuta</i>	<i>Chlidonias niger</i>
<i>Anas crecca</i>	<i>Chroicocephalus genei</i>
<i>Anas platyrhynchos</i>	<i>Chroicocephalus ridibundus</i>
<i>Anser anser</i>	<i>Ciconia ciconia</i>
<i>Anthus spinoletta</i>	<i>Ciconia nigra</i>
<i>Apus apus</i>	<i>Cinclus cinclus</i>
<i>Apus melba</i>	<i>Circus aeruginosus</i>
<i>Aquila heliaca</i>	<i>Circus macrourus</i>
<i>Ardea alba</i>	<i>Circus pygargus</i>
<i>Ardea cinerea</i>	<i>Clamator glandarius</i>
<i>Ardea purpurea</i>	<i>Corvus cornix</i>
<i>Ardeola ralloides</i>	<i>Coturnix coturnix</i>
<i>Asio flammeus</i>	<i>Crex crex</i>
<i>Asio otus</i>	<i>Cuculus canorus</i>
<i>Aythya ferina</i>	<i>Delichon urbicum</i>
<i>Aythya fuligula</i>	<i>Dryobates minor</i>
<i>Aythya nyroca</i>	<i>Egretta garzetta</i>
<i>Botaurus stellaris</i>	<i>Emberiza schoeniclus</i>
<i>Bubulcus ibis</i>	<i>Oenanthe oenanthe</i>

Table A.2 (continued)	
<i>Burhinus oedicnemus</i>	<i>Oxyura leucocephala</i>
<i>Falco subbuteo</i>	<i>Panurus biarmicus</i>
<i>Fulica atra</i>	<i>Passer domesticus</i>
<i>Gallinago gallinago</i>	<i>Pelecanus crispus</i>
<i>Gallinula chloropus</i>	<i>Pelecanus onocrotalus</i>
<i>Gelochelidon nilotica</i>	<i>Phalacrocorax carbo</i>
<i>Glareola pratincola</i>	<i>Phoenicopterus roseus</i>
<i>Grus grus</i>	<i>Phylloscopus collybita</i>
<i>Haematopus ostralegus</i>	<i>Platalea leucorodia</i>
<i>Haliaeetus albicilla</i>	<i>Plegadis falcinellus</i>
<i>Himantopus himantopus</i>	<i>Podiceps cristatus</i>
<i>Hirundo rustica</i>	<i>Podiceps grisegena</i>
<i>Hydroprogne caspia</i>	<i>Podiceps nigricollis</i>
<i>Ichthyaetus melanocephalus</i>	<i>Ptyonoprogne rupestris</i>
<i>Ixobrychus minutus</i>	<i>Rallus aquaticus</i>
<i>Lanius collurio</i>	<i>Recurvirostra avosetta</i>
<i>Larus armenicus</i>	<i>Remiz pendulinus</i>
<i>Larus michahellis</i>	<i>Riparia riparia</i>
<i>Locustella luscinioides</i>	<i>Saxicola rubicola</i>
<i>Mareca strepera</i>	<i>Spatula clypeata</i>
<i>Marmaronetta angustirostris</i>	<i>Spatula querquedula</i>
<i>Merops apiaster</i>	<i>Sterna hirundo</i>
<i>Microcarbo pygmaeus</i>	<i>Sternula albifrons</i>
<i>Milvus migrans</i>	<i>Sturnus vulgaris</i>
<i>Motacilla alba</i>	<i>Sylvia curruca</i>
<i>Motacilla cinerea</i>	<i>Tachybaptus ruficollis</i>
<i>Motacilla citreola</i>	<i>Tadorna ferruginea</i>
<i>Motacilla flava</i>	<i>Tadorna tadorna</i>
<i>Neophron percnopterus</i>	<i>Tringa totanus</i>
<i>Netta rufina</i>	<i>Vanellus leucurus</i>
<i>Nycticorax nycticorax</i>	<i>Vanellus spinosus</i>
<i>Falco cherrug</i>	<i>Vanellus vanellus</i>
<i>Falco peregrinus</i>	<i>Zapornia parva</i>

The 27 species that have gone extinct were Black Tern (*Chlidonias niger*), Caspian Tern (*Hydroprogne caspia*), Common Crane (*Grus grus*), Common Kingfisher (*Alcedo atthis*), Common Sandpiper (*Actitis hypoleucos*), Common Snipe (*Gallinago gallinago*), Corn Crake (*Crex crex*), Dalmatian Pelican (*Pelecanus*

crispus), Eurasian Oystercatcher (*Haematopus ostralegus*) Eurasian Teal (*Anas crecca*), Ferruginous Duck (*Aythya nyroca*), Gadwall (*Mareca strepera*), Great White Pelican (*Pelecanus onocrotalus*), Little Crake (*Zapornia parva*), Marbled Teal (*Marmaronetta angustirostris*), Moustached Warbler (*Acrocephalus melanopogon*), Northern Pintail (*Anas acuta*), Pygmy Cormorant (*Microcarbo pygmaeus*), Red-necked Grebe (*Podiceps grisegena*), Rufous-tailed Scrub Robin (*Cercotrichas galactotes*), Saker Falcon (*Falco cherrug*), Savi's Warbler (*Locustella luscinioides*), Short-eared Owl (*Asio flammeus*), Tufted Duck (*Aythya fuligula*), Water Pipit (*Anthus spinoletta*), White-tailed Eagle (*Haliaeetus albicilla*), and White-winged Tern (*Chlidonias leucopterus*).

Species that have colonized the basin were Cattle Egret (*Bubulcus ibis*), Great Cormorant (*Phalacrocorax carbo*), White-tailed Lapwing (*Vanellus leucurus*), and Yellow-legged Gull (*Larus michahellis*).

A.3 Functional traits

I used *corrplot* function from the *corrplot* R package (Wei et al. 2017) to generate correlation matrices visualizing Spearman's Rho (Borcard et al. 2018) for the binary traits and continuous traits. To check the correlation between binary and continuous traits, I used point biserial correlation coefficient (Tate 1954). Finally, to check the relationship between our only categorical trait, early developmental mode, and the other traits, I used generalized linear models (Zuur et al., 2009). I eliminated traits that were significantly and strongly (threshold $p:0.70$ - inclusive) correlated with the others. When choosing between two correlated traits to eliminate one, I chose the one that had higher correlation coefficients with the other traits. None of the traits were found to be significantly associated with any of the levels of our categorical trait. In the end, I had to remove a total of 13 traits/trait levels, which were nesting substrate: ground-open, nesting behaviour: solitary, breeding habitat: urban-suburban, body length, bill length, wing length, incubation duration, broods per year, and generation length. This left us with 74 traits/trait levels to work with. The

detailed descriptions of each trait, their ecological relevance, sources I used to score them, along with the description of their levels are given below.

For the traits that were scored as non-mutually exclusive binary traits such as breeding habitat, levels that are not applicable to our study area (e.g., our study area has no sea habitats) were excluded from the study. So were the traits or trait levels that had the same score for all of the species (in order not to artificially inflate the functional similarities). I used locally-collected data from Kirwan et al. (2008) whenever relevant to increase the representativeness of our trait-based analyses. These traits were broods per year, reproductive effort, migratory strategy, nesting substrate, nesting substrate plasticity, egg laying season, egg laying season length, breeding habitat, and breeding habitat plasticity.

Body mass

Sources: Dunning (2007), Wilman et al. (2014).

Definition: This continuous numeric trait gives the mean body mass of bird species in grams.

Ecological relevance: Resource use, energy requirements, rate of resource consumption, resource quantity, temperature tolerance, thermoregulation, dispersal ability, dispersal distance, prey type, trophic position, metabolic rate, home range size, longevity, flight performance, response to changes in the environment and disturbances, contribution to ecosystem functions (such as seed dispersal and pest control, resource transportation), habitat use, fitness (via survival and growth), species interactions (such as plant-frugivore), foraging behaviour, energy flow in the food web.

Body length

Sources: Storchová & Hořák (2018).

Definition: This continuous numeric trait gives the mean body length of the birds in cm.

Ecological relevance: Metabolic rate, territory size, foraging behaviour, longevity, home-range size, resource use, habitat use, foraging substrate, dispersal capacity, energy requirement, aerial agility, and flight capacity.

Wing length

Sources: Storchová and Hořák (2018).

Definition: This continuous numeric trait gives the mean wing length of the birds in mm.

Ecological relevance: Flight capacity, energy requirement, maneuverability, spatial distribution of resource use, and capacity to respond to changes in the environment and disturbances.

Bill length

Sources: Storchová and Hořák (2018).

Definition: This continuous numeric trait gives the mean bill length of the birds in mm.

Ecological relevance: Diet specialization, habitat use, thermoregulation, propagule dispersal, foraging behaviour, foraging substrate, food type, trophic niche, species interactions, pollination, and resource partitioning.

Tarsus length

Sources: Storchová and Hořák (2018).

Definition: This continuous numeric trait gives the mean tarsus length of the birds in mm.

Ecological relevance: Bipedal movement capacity, habitat use, foraging habitat use, foraging substrate, resource accessibility, foraging behaviour, predator avoidance.

Relative brain mass

Sources: Galván & Møller (2011), Garamszegi et al. (2002), Iwaniuk (2004), Jiménez-Ortega et al. (2020), Minias & Podlaszczuk (2017), Sayol et al. (2020), Sol et al. (2010), Tsuboi et al. (2018).

Definition: I used residuals from brain mass ~ body mass regression to control for the allometric relationship between body mass and brain and to obtain a trait that represents the change in brain mass that is not solely explained by changes in body mass. For the purpose, I built a gamma GLM with log link by using the *glmmTMB* function from *glmmTMB* package (Brooks et al. 2017) in R software (R Core Team 2021). For each species, the trait score was the residual for that data point. The model was validated as the other models (see section S7). R-squared value for the model was 0.94. The trait is a continuous numeric one.

Ecological relevance: Capacity to adapt to novel environments, adaptability, response to changes in environment and disturbances, behavioural flexibility.

Sexual dimorphism

Sources: Storchová & Hořák (2018).

Definition: This continuous numeric trait was calculated as male body mass divided by female body mass.

Ecological relevance: Response to the changes in the environment and disturbances, resilience, recovery ability, niche divergence between the sexes.

Clutch size

Sources: Storchová & Hořák (2018).

Definition: This continuous numeric trait gives the mean clutch size of a species.

Ecological relevance: Energy requirement, resource quantity, response to the changes in the environment and disturbances, recovery ability, energy and matter turnover rate, fitness (via growth, reproduction, and survival), reproductive potential, rate of colonization, longevity, reproductive effort.

Broods per year

Sources: Storchová & Hořák (2018), Kirwan et al. (2008).

Definition: This continuous numeric trait gives the mean number of broods per year.

Ecological relevance: Response to changes in the environment and disturbances, resilience, recovery ability, invasion success. F_{β}

Reproductive effort

Sources: Storchová & Hořák (2018), Kirwan et al. (2008).

Definition: I calculated reproductive effort as (Mean number of broods per year x mean clutch size x mean egg mass) / mean female body mass. Thus, this continuous numeric trait is a measure of reproductive effort by the females of a species.

Ecological relevance: Response to changes in the environment and disturbances, resilience, recovery ability, invasion success.

Early developmental mode

Sources: Storchová & Hořák (2018).

Definition: This categorical trait gives developmental mode of the young of a species.

Ecological relevance: Energy requirement, resource quantity, response to the changes in the environment and disturbances, fitness (via growth, reproduction, and survival), temporal resource use.

Levels:

I) Altricial: Chicks hatch naked and relatively undeveloped (Lovette & Fitzpatrick, 2016)

II) Semi-altricial: Mid-way between altricial and precocial. Chicks hatch covered with down, capacity to leave the nest, but they are fed by their parent.

III) Precocial: Chicks hatch with a high degree of independence on the parents, well-feathered with down and with some locomotory, thermoregulatory capabilities (Lovette & Fitzpatrick, 2016)

Social behavior during breeding season

Sources: Storchová & Hořák (2018).

Definition: Sociality of the species during breeding season. The trait was scored as non-mutually exclusive binary traits.

Ecological relevance: Response to the changes in the environment and disturbances, predator avoidance, resource use, pest control, spatial distribution of resource use, nutrient transportation, propagule dispersal

Levels:

I) Colonial: Species breeding in colonies.

II) Semi-colonial: Some individuals choose to breed solitarily, while some breed in colonies.

III) Solitary: Species breeding in isolation.

Incubation duration

Sources: Storchová & Hořák (2018).

Definition: This discrete numeric trait represents mean duration of incubation in days.

Ecological relevance: Temporal resource use, fitness, energy requirement, reproductive effort, spatial distribution of resource use, response to changes in the environment and disturbances, resilience

Fledgling duration

Sources: Storchová & Hořák (2018).

Definition: This discrete numeric trait represents the mean time (in days) it takes for the offspring of a species to fledge.

Ecological relevance: Temporal resource use, response to changes in the environment and disturbances

Age at first reproduction

Sources: Palomino et al. (1999), Storchová & Hořák (2018)

Definition: This continuous numeric trait shows the mean age at which a species becomes sexually mature.

Ecological relevance: Influences population dynamics, responses to changes in the environment, temporal resource use and invasion success. Also influences fitness via affecting growth, survival, and reproduction.

Daily activity period

Sources: Pearman et al. (2014)

Definition: Time(s) of the day during which a species is known to be active. The trait was scored as non-mutually exclusive binary traits.

Ecological relevance: Resource use, temporal resource use, niche partitioning.

Levels:

I) Diurnal: Species that are active during the day.

II) Crepuscular: Species that are active during the dusk and dawn.

III) Nocturnal: Species that are active during the night.

Daily activity period plasticity

Sources: Pearman et al. (2014)

Definition: This discrete numeric trait is a measure of how plastic a species about the timing of their activities. I calculated daily activity period plasticity as the number of levels of daily activity period used by a species. For example, if a species gets a “yes” for diurnal and crepuscular levels of daily activity period traits, then its daily activity period plasticity score is $1+1 = 2$.

Ecological relevance: Resilience, response to changes in the environment and disturbances, adaptability, competitive ability, temporal niche use.

Generation length

Sources: BirdLife International (2021)

Definition: Mean generation length of a species. This trait was scored as a continuous numeric trait.

Ecological relevance: Temporal resource use, response to changes in the environment and disturbances, recovery ability, resilience.

Diet

Sources: Wilman et al. (2014).

Definition: Diet of a species. I have binarized the percentage data provided in Wilman et al. (2014) because relative amount of a dietary item can change substantially from one place to another (Cramp 1977). This decision may have resulted in some information loss, but I believe it is better to lose some information than to include false or non-representative information. The trait was scored as non-mutually exclusive binary traits.

Ecological relevance: Nutrient transportation, nutrient cycling, ecosystem services (such as pollination, seed dispersal, pest control), habitat use, niche partitioning, foraging behaviour, response to changes in the environment and disturbance, energy requirement, trophic position, energy flow in the food web, invasion success.

Levels:

I) Invertebrates: All kinds of invertebrates (terrestrial and aquatic).

II) Endothermic vertebrates: Warm-blooded vertebrates.

III) Ectothermic vertebrates: Cold-blooded vertebrates.

IV) Fish: All kinds of fish.

V) Carcass: Dead bodies of other organisms.

VI) Fruits: Fruits of all kinds (terrestrial and aquatic).

VII) Seeds: Seeds of plants (terrestrial and aquatic).

VIII) Vegetative parts of plants: Vegetative parts of plants (terrestrial and aquatic).

Diet plasticity

Sources: Wilman et al. (2014).

Definition: This discrete numeric trait is a measure of how plastic a species about their dietary items. I calculated diet plasticity as the number of levels of diet trait used by a species. For example, if a species gets a “yes” for seeds and fruits for the diet trait, then its diet plasticity score is $1+1 = 2$.

Ecological relevance: Capacity to adapt to novel environments, adaptability, response to changes in environment and disturbances, nutrient transportation, nutrient cycling, ecosystem services (such as pollination, seed dispersal, pest control), invasion success, energy flow in the food web

Foraging substrate/stratum

Sources: Wilman et al. (2014)

Definition: Foraging stratum or substrate (within in a habitat) used by a species. The trait was scored as non-mutually exclusive binary traits. The data coming from Wilman et al. (2014) was in the form of percentages, and once again, I decided to binarize the data because the relative importance and use frequency of foraging substrates can change from one place to another (Cramp 1977). This resulted in some information loss, but I believe it is better to lose some information than having some non-representative information.

Ecological relevance: Resource use, response to changes in the environment and disturbances, niche partitioning, nutrient transportation, propagule dispersal.

Levels:

I) Water (below surface): Water column, below the surface. Includes bottom feeding.

II) Water (around surface): Around the surface in water.

III) Ground: Ground of all types.

IV) Understory: Understory in a forest/woodland.

V) Forest (mid-high): Mid stratum in a forest/woodland.

VI) Canopy: Canopy in a forest/woodland.

VII) Aerial: Air.

VIII) Pelagic: Open water.

Foraging substrate/stratum plasticity

Sources: Wilman et al. (2014)

Definition: This discrete numeric trait is a measure of how plastic a species about the substrate they use to forage. I calculated foraging substrate/stratum plasticity as the number of levels of foraging substrate/stratum used by a species. For example, if a species gets a “yes” for aerial and ground levels for foraging substrate/stratum trait, then its foraging substrate/stratum plasticity score is $1+1 = 2$.

Ecological relevance: Propagule dispersal, response to changes in the environment and disturbances, ecosystem services (e.g. seed dispersal, pollination), adaptability, niche partitioning, invasion success.

Territoriality

Sources: Storchová & Hořák (2018).

Definition: This binary trait shows whether a species is territorial during breeding season or not.

Ecological relevance: Spatial distribution of resource use, pest control, propagule dispersal, response to the changes in the environment and disturbances.

Foraging behavior

Sources: Cramp (1977), Pearman et al. (2014)

Definition: Foraging behaviour and manoeuvres used by a species to acquire its food. This trait was scored as non-mutually exclusive binary traits.

Ecological relevance: Resource use, trophic position, ecosystem services (e.g., pest control, seed dispersal, pollination), propagule dispersal, niche partitioning, response to changes in the environment and disturbances, energy requirement, habitat use.

Levels:

I) Pursuit (air or aquatic): Chasing prey actively in air or in water.

II) Sally: Sallying or suddenly attacking or charging.

III) Foliage glean: Gleaning from foliage.

IV) Pounce: Springing or swooping quickly to catch prey.

V) Graze: Eating vegetation, grass (terrestrial).

VI) Peck: Pecking to catch prey.

VII) Dig: Digging to catch prey.

VIII) Overturn: Overturning objects to look for prey.

IX) Probe: Probing soil or mud to catch prey.

Foraging behavior plasticity

Sources: Cramp (1977), Pearman et al. (2014)

Definition: This discrete numeric trait is a measure of how plastic a species is about the behaviors used in foraging. I calculated foraging behaviour plasticity as the number of levels of foraging behaviors used by a species. For example, if a species gets a “yes” for sally and peck for foraging behaviour trait, then its foraging behaviour plasticity score is $1+1 = 2$.

Ecological relevance: Response to changes in the environment and disturbances, niche partitioning.

Migratory strategy

Sources: Cornell Lab of Ornithology (2021), Kirwan et al. (2008)

Definition: This binary trait shows whether a species is a summer visitor in the study area (Konya Closed Basin) or a resident. Scoring was done by using locally collected data.

Ecological relevance: Resource use, energy requirement, spatial distribution of resource use, temporal resource use, propagule dispersal, nutrient transportation, response to changes in the environment and disturbances, pollination

Egg laying season

Sources: Cornell Lab of Ornithology (2021), Cramp (1977), Kirwan et al. (2008)

Definition: Spring and summer months were divided into halves: first half and second half. The trait shows whether populations of a species lay in a given time period in the study area (Konya Closed Basin). This trait was scored using locally collected data as non-mutually exclusive binary traits. I did not include replacement clutches in our scoring.

Ecological relevance: Resource use, temporal resource use, response to changes in the environment (such as climate change) and disturbances.

Egg laying season length/plasticity

Sources: Cornell Lab of Ornithology (2021), Cramp (1977), Kirwan et al. (2010)

Definition: This discrete numeric trait represents the length the laying season for a species in study area (Konya Closed Basin). If a species lays in the first half of April, second half of April, and first half of May, then it gets a $1+1+1 = 3$ score for this trait.

Ecological relevance: Adaptability, response to changes in the environment (such as climate change) and disturbances.

Breeding habitat

Sources: Cramp (1977), Kear (2005), Kirwan et al. (2008), Pearman et al. (2014)

Definition: The species' breeding environment (Whittaker, Levin & Root, 1973). One habitat can include multiple types of nesting substrates (see below). For example, two species may be breeding within a deciduous forest and one of them may be nesting on tree branches, while the other nests in the shrubs of the understory. The trait was scored as non-mutually exclusive binary traits.

Ecological relevance: Related to resource transportation, capacity to respond to changes in the environment and disturbances, resource use, niche partitioning.

Levels:

I) Woodland: Forests and small stands of all kinds. Includes open forests and plantations.

II) Streams: Streams, rivers, waterways.

III) Shrubland: Landscape dominated by shrubs and bushes.

IV) Cultivated land: All kinds of cultivated fields.

V) Grassland: Includes steppe, dry grassland and meadows.

VI) Wetland: Includes lakes (both brackish and freshwater), ponds, marshes, saltpans, and reservoirs.

VII) Urban/Suburban: Human settlements of different sizes. Includes villages, towns, and cities.

VIII) Montane: Includes alpine and subalpine parts of mountains and mountain hillsides.

Breeding habitat plasticity

Sources: Cramp (1977), Kear (2005), Kirwan et al. (2008), Pearman et al. (2014)

Definition: This discrete numeric trait represents the number of different habitats used by a species in study area (Konya Closed Basin). If a species breeds in woodland, streams and wetlands, then it gets a $1+1+1 = 3$ score for this trait.

Ecological relevance: Habitat use, resource transportation, response to changes in the environment and disturbances, resource use, niche partitioning.

Nesting substrate/stratum

Sources: Cramp (1977), Kear (2005), Kirwan et al. (2008), Pearman et al. (2014)

Definition: Substrate on which the nest is built upon or in. The trait was scored as non-mutually exclusive binary traits.

Ecological relevance: Related to micro-habitat use, resource requirement, capacity to respond to changes in the environment and disturbances, and predator avoidance.

Levels:

I) Ground open: Bare ground. Includes all kinds of bare (i.e., “plantless”) surfaces such as mud, gravel beaches.

II) Ground hole: Holes in the ground. Includes dug holes as well as mammal holes that are used as nest sites.

III) Tree open: All parts of a tree except within its timber (i.e., holes). Attached nests are included in this level

IV) Tree hole: Tree holes. Includes holes made by woodpeckers.

V) Reeds: Includes reeds and cattails of all kinds.

VI) Artificial surfaces: Man-made structures and surfaces such as buildings, bridges, electric polls.

VII) Sand banks: Sand banks produced by the action of wind or water erosion.

VIII) Shrub: Within or underneath a shrub or bush.

IX) Island: Islands in wetlands.

X) Herbaceous: All kinds of dense and sparse herbaceous, low-lying vegetation. Includes Salicornia matts.

XI) Cliffs and rocky outcrops: Includes both rocky cliffs of all sizes and rocky outcrops.

XII) Floating vegetation: Matts of floating vegetation such as water lilies.

XIII) Brood parasite: Not a substrate, but a very relevant level. Brood parasites do not build nests; they lay their eggs inside their hosts' nests.

Nesting substrate/stratum plasticity

Sources: Cramp (1977), Kear (2005), Kirwan et al. (2008), Pearman et al. (2014)

Definition: This discrete numeric trait represents the number of substrates used by a species to nest in the study area (Konya Closed Basin). If a species nests on islands or on artificial surfaces, then it gets a $1+1 = 2$ score for this trait.

Ecological relevance: Habitat use, resource transportation, response to changes in the environment and disturbances, resource use, niche partitioning.

A.4 Functional beta diversity

In taxonomical context, total pairwise beta diversity, which I measured as Sorensen pairwise dissimilarity, is defined as the ratio of the sum of the number of unique species in the two communities (b and c) to the sum of the number of unique species in the two communities and twice the number of shared species (a) (1). The functional counterpart of that, total pairwise functional β diversity can be obtained simply by replacing a with the volume of functional space shared between the two communities ($V(C_1 \cap C_2)$ where $V(C_1)$ and $V(C_2)$ are trait space volumes occupied by individual communities) or functional similarity (Villéger et al. 2011), and b and c with non-overlapping parts of the communities' functional volumes ($V(C_1) - V(C_1 \cap C_2)$ and $V(C_2) - V(C_1 \cap C_2)$; Baselga & Orme, 2012; Bevilacqua & Terlizzi, 2020; Figure A.4.1) or functional dissimilarity (Villéger et al. 2011).

$$\beta_{SOR} = \frac{b+c}{2a+b+c} = \underbrace{\left(\frac{\min(b,c)}{a+\min(b,c)} \right)}_{F_{\beta_{SIM}}^*} + \underbrace{\left(\frac{\max(b,c) - \min(b,c)}{2a+\min(b,c)+\max(b,c)} \cdot \frac{a}{a+\min(b,c)} \right)}_{F_{\beta_{SNE}}^*} \quad (1)$$

* For $F_{\beta_{SOR}} \rightarrow a = V(C_1 \cap C_2)$, $b = V(C_1) - V(C_1 \cap C_2)$, $c = V(C_2) - V(C_1 \cap C_2)$

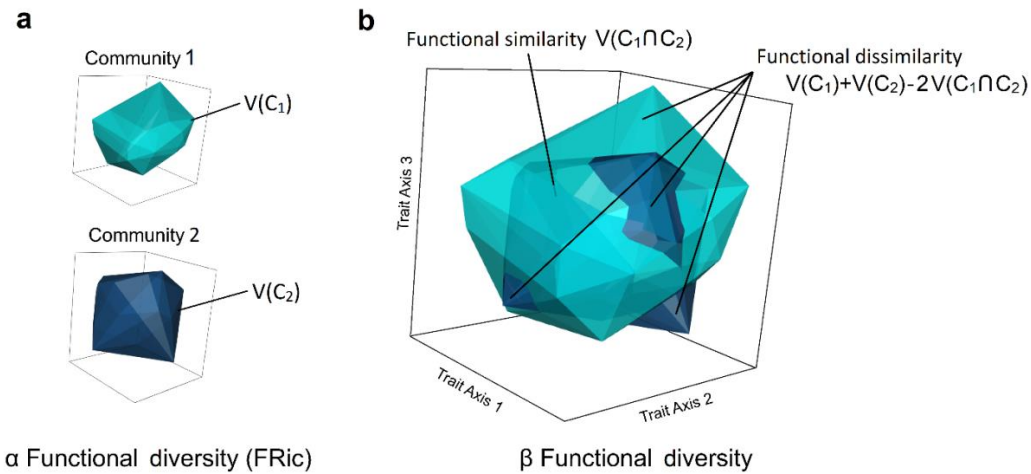


Figure A.4.1 α and β functional diversity. Convex hull volumes, or Functional Richness (FRic) of two hypothetical communities ($V(C_1)$ and $V(C_2)$) in three-dimensional functional space (a), and the pairwise functional similarity ($V(C_1 \cap C_2)$) and functional dissimilarity ($V(C_1) + V(C_2) - 2V(C_1 \cap C_2)$) (b). See in conjunction with (1).

A.5 Model summary table

Table A.5.1 Model IDs, error distributions (Error dist.), link functions (Link func.), estimated regression parameters, standard errors (Std. error), p -values, and random effect variance estimates (σ of random effect) of the statistical models built. FRic: Functional richness.

Model ID	Error dist.	Link func.		Estimate	Std. error	p -value	σ of the random effect
I - α Species richness	Neg. bin.	Log	Intercept	3.246	0.171	***	
			<i>Fixed effects</i> Year 2018	-0.915	0.139	***	
			<i>Random effects</i> Area				0.424
			<i>Random effects</i> Square ID				0.150
II - α Functional richness	Gamma	Log	Intercept	-4.506	0.2023	***	
			<i>Fixed effects</i> Year 2018	-0.6847	0.2861	*	
			<i>Random effects</i> Square ID				3.72E-09

A.6 R code for reproducible analyses

The code can be accessed at <https://github.com/whiteheadedduck/wetlandbirds>.



B. Appendix for Chapter 2

B.1 Species list

A full list of species included in this chapter is given in Table B.1. See section 2.2.3.1 for more information about the taxonomic code used.

Table B.1 List of species included in this chapter. See section 2.2.3.1 for more information about the taxonomic code used.

<i>Acanthis flammea/hornemanni</i>	<i>Gyps fulvus</i>
<i>Accipiter brevipes</i>	<i>Haematopus ostralegus</i>
<i>Accipiter gentilis</i>	<i>Haliaeetus albicilla</i>
<i>Accipiter nisus</i>	<i>Hieraaetus pennatus</i>
<i>Acrocephalus agricola</i>	<i>Himantopus himantopus</i>
<i>Acrocephalus arundinaceus</i>	<i>Hippolais icterina</i>
<i>Acrocephalus dumetorum</i>	<i>Hippolais olivetorum</i>
<i>Acrocephalus melanopogon</i>	<i>Hippolais polyglotta</i>
<i>Acrocephalus paludicola</i>	<i>Hirundo rustica</i>
<i>Acrocephalus palustris</i>	<i>Histrionicus histrionicus</i>
<i>Acrocephalus schoenobaenus</i>	<i>Hydrocoloeus minutus</i>
<i>Acrocephalus scirpaceus</i>	<i>Hydroprogne caspia</i>
<i>Actitis hypoleucos</i>	<i>Ichthyaetus melanocephalus</i>
<i>Aegithalos caudatus</i>	<i>Iduna opaca/pallida</i>
<i>Aegolius funereus</i>	<i>Ixobrychus minutus</i>
<i>Aegypius monachus</i>	<i>Jynx torquilla</i>
<i>Alauda arvensis</i>	<i>Lagopus lagopus</i>
<i>Alaudala heinei/rufescens</i>	<i>Lagopus muta</i>
<i>Alcedo atthis</i>	<i>Lanius collurio</i>
<i>Alectoris barbara</i>	<i>Lanius excubitor/meridionalis</i>
<i>Alectoris chukar</i>	<i>Lanius minor</i>
<i>Alectoris graeca</i>	<i>Lanius nubicus</i>
<i>Alectoris rufa</i>	<i>Lanius senator</i>
<i>Anas acuta</i>	<i>Larus argentatus/cachinnans</i>
<i>Anas crecca</i>	<i>Larus canus</i>
<i>Anas platyrhynchos</i>	<i>Larus fuscus</i>
<i>Anser anser</i>	<i>Larus michahellis</i>

Table B.1 (continued)

<i>Anser brachyrhynchus</i>	<i>Limosa lapponica</i>
<i>Anser erythropus</i>	<i>Limosa limosa</i>
<i>Anser fabalis</i>	<i>Linaria cannabina</i>
<i>Anthropoides virgo</i>	<i>Linaria flavirostris</i>
<i>Anthus campestris</i>	<i>Locustella fluviatilis</i>
<i>Anthus cervinus</i>	<i>Locustella luscinioides</i>
<i>Anthus petrosus</i>	<i>Locustella naevia</i>
<i>Anthus pratensis</i>	<i>Lophophanes cristatus</i>
<i>Anthus spinoletta</i>	<i>Loxia curvirostra</i>
<i>Anthus trivialis</i>	<i>Loxia leucoptera</i>
<i>Apus apus</i>	<i>Loxia pytyopsittacus</i>
<i>Apus caffer</i>	<i>Loxia scotica</i>
<i>Apus pallidus</i>	<i>Lullula arborea</i>
<i>Aquila adalberti</i>	<i>Luscinia luscinia</i>
<i>Aquila chrysaetos</i>	<i>Luscinia megarhynchos</i>
<i>Aquila fasciata</i>	<i>Luscinia svecica</i>
<i>Aquila heliaca</i>	<i>Lymnocyptes minimus</i>
<i>Ardea alba</i>	<i>Lyrurus tetrix</i>
<i>Ardea cinerea</i>	<i>Mareca penelope</i>
<i>Ardea purpurea</i>	<i>Mareca strepera</i>
<i>Ardeola ralloides</i>	<i>Marmaronetta angustirostris</i>
<i>Arenaria interpres</i>	<i>Melanitta fusca</i>
<i>Asio flammeus</i>	<i>Melanitta nigra</i>
<i>Asio otus</i>	<i>Melanocorypha calandra</i>
<i>Athene noctua</i>	<i>Mergellus albellus</i>
<i>Aythya ferina</i>	<i>Mergus merganser</i>
<i>Aythya fuligula</i>	<i>Mergus serrator</i>
<i>Aythya marila</i>	<i>Merops apiaster</i>
<i>Aythya nyroca</i>	<i>Microcarbo pygmaeus</i>
<i>Bombycilla garrulus</i>	<i>Milvus migrans</i>
<i>Botaurus stellaris</i>	<i>Milvus milvus</i>
<i>Branta bernicla</i>	<i>Monticola saxatilis</i>
<i>Branta leucopsis</i>	<i>Monticola solitarius</i>
<i>Bubo bubo</i>	<i>Montifringilla nivalis</i>
<i>Bubo scandiacus</i>	<i>Motacilla alba</i>
<i>Bubulcus ibis</i>	<i>Motacilla cinerea</i>
<i>Bucanetes githagineus</i>	<i>Motacilla citreola</i>

Table B.1 (continued)

<i>Bucephala clangula</i>	<i>Motacilla flava</i>
<i>Bucephala islandica</i>	<i>Muscicapa striata</i>
<i>Burhinus oedicephalus</i>	<i>Neophron percnopterus</i>
<i>Buteo buteo</i>	<i>Netta rufina</i>
<i>Buteo lagopus</i>	<i>Nucifraga caryocatactes</i>
<i>Buteo rufinus</i>	<i>Numenius arquata</i>
<i>Calandrella brachydactyla</i>	<i>Numenius phaeopus</i>
<i>Calcarius lapponicus</i>	<i>Nycticorax nycticorax</i>
<i>Calidris alpina</i>	<i>Oenanthe hispanica/melanoleuca</i>
<i>Calidris falcinellus</i>	<i>Oenanthe isabellina</i>
<i>Calidris maritima</i>	<i>Oenanthe leucura</i>
<i>Calidris minuta</i>	<i>Oenanthe oenanthe</i>
<i>Calidris pugnax</i>	<i>Oenanthe pleschanka</i>
<i>Calidris temminckii</i>	<i>Oriolus oriolus</i>
<i>Caprimulgus europaeus</i>	<i>Otis tarda</i>
<i>Caprimulgus ruficollis</i>	<i>Otus scops</i>
<i>Carduelis carduelis</i>	<i>Oxyura leucocephala</i>
<i>Carduelis citrinella</i>	<i>Pandion haliaetus</i>
<i>Carpodacus erythrinus</i>	<i>Panurus biarmicus</i>
<i>Cecropis daurica</i>	<i>Parus major</i>
<i>Cercotrichas galactotes</i>	<i>Passer domesticus</i>
<i>Certhia brachydactyla</i>	<i>Passer hispaniolensis</i>
<i>Certhia familiaris</i>	<i>Passer italiae</i>
<i>Cettia cetti</i>	<i>Passer montanus</i>
<i>Charadrius alexandrinus</i>	<i>Pastor roseus</i>
<i>Charadrius dubius</i>	<i>Pelecanus crispus</i>
<i>Charadrius hiaticula</i>	<i>Pelecanus onocrotalus</i>
<i>Chersophilus duponti</i>	<i>Perdix perdix</i>
<i>Chlidonias hybrida</i>	<i>Periparus ater</i>
<i>Chlidonias leucopterus</i>	<i>Perisoreus infaustus</i>
<i>Chlidonias niger</i>	<i>Pernis apivorus</i>
<i>Chloris chloris</i>	<i>Petronia petronia</i>
<i>Chroicocephalus genei</i>	<i>Phalacrocorax carbo</i>
<i>Chroicocephalus ridibundus</i>	<i>Phalaropus fulicarius</i>
<i>Ciconia ciconia</i>	<i>Phalaropus lobatus</i>
<i>Ciconia nigra</i>	<i>Phoenicopertus roseus/ruber</i>
<i>Cinclus cinclus</i>	<i>Phoenicurus ochruros</i>

Table B.1 (continued)

<i>Circaetus gallicus</i>	<i>Phoenicurus phoenicurus</i>
<i>Circus aeruginosus</i>	<i>Phylloscopus bonelli/orientalis</i>
<i>Circus cyaneus</i>	<i>Phylloscopus borealis</i>
<i>Circus macrourus</i>	<i>Phylloscopus collybita/ibericus</i>
<i>Circus pygargus</i>	<i>Phylloscopus sibilatrix</i>
<i>Cisticola juncidis</i>	<i>Phylloscopus trochiloides</i>
<i>Clamator glandarius</i>	<i>Phylloscopus trochilus</i>
<i>Clanga clanga</i>	<i>Pica pica</i>
<i>Clanga pomarina</i>	<i>Picoides tridactylus</i>
<i>Clangula hyemalis</i>	<i>Picus canus</i>
<i>Coccothraustes coccothraustes</i>	<i>Picus sharpei/viridis</i>
<i>Columba livia</i>	<i>Pinicola enucleator</i>
<i>Columba oenas</i>	<i>Platalea leucorodia</i>
<i>Columba palumbus</i>	<i>Plectrophenax nivalis</i>
<i>Coracias garrulus</i>	<i>Plegadis falcinellus</i>
<i>Corvus corax</i>	<i>Pluvialis apricaria</i>
<i>Corvus cornix/corone</i>	<i>Podiceps auritus</i>
<i>Corvus frugilegus</i>	<i>Podiceps cristatus</i>
<i>Corvus monedula</i>	<i>Podiceps grisegena</i>
<i>Coturnix coturnix</i>	<i>Podiceps nigricollis</i>
<i>Crex crex</i>	<i>Poecile cinctus</i>
<i>Cuculus canorus</i>	<i>Poecile lugubris</i>
<i>Curruca balearica/sarda</i>	<i>Poecile montanus</i>
<i>Curruca cantillans/iberiae/subalpina</i>	<i>Poecile palustris</i>
<i>Curruca communis</i>	<i>Porphyrio porphyrio</i>
<i>Curruca conspicillata</i>	<i>Porzana porzana</i>
<i>Curruca crassirostris/hortensis</i>	<i>Prunella collaris</i>
<i>Curruca curruca</i>	<i>Prunella modularis</i>
<i>Curruca melanocephala</i>	<i>Pterocles alchata</i>
<i>Curruca nisoria</i>	<i>Pterocles orientalis</i>
<i>Curruca ruppeli</i>	<i>Ptyonoprogne rupestris</i>
<i>Curruca undata</i>	<i>Pyrrhocorax graculus</i>
<i>Cyanistes caeruleus</i>	<i>Pyrrhocorax pyrrhocorax</i>
<i>Cyanistes cyaneus</i>	<i>Pyrrhula pyrrhula</i>
<i>Cyanopica cooki</i>	<i>Rallus aquaticus</i>
<i>Cygnus cygnus</i>	<i>Recurvirostra avosetta</i>
<i>Cygnus olor</i>	<i>Regulus ignicapilla</i>

Table B.1 (continued)

<i>Delichon urbicum</i>	<i>Regulus regulus</i>
<i>Dendrocopos leucotos</i>	<i>Remiz pendulinus</i>
<i>Dendrocopos major</i>	<i>Riparia riparia</i>
<i>Dendrocopos syriacus</i>	<i>Saxicola rubetra</i>
<i>Dendrocoptes medius</i>	<i>Saxicola rubicola</i>
<i>Dryobates minor</i>	<i>Scolopax rusticola</i>
<i>Dryocopus martius</i>	<i>Serinus serinus</i>
<i>Egretta garzetta</i>	<i>Sitta europaea</i>
<i>Elanus caeruleus</i>	<i>Sitta krueperi</i>
<i>Emberiza aureola</i>	<i>Sitta neumayer</i>
<i>Emberiza caesia</i>	<i>Sitta whiteheadi</i>
<i>Emberiza calandra</i>	<i>Spatula clypeata</i>
<i>Emberiza cia</i>	<i>Spatula querquedula</i>
<i>Emberiza cineracea</i>	<i>Spinus spinus</i>
<i>Emberiza cirrus</i>	<i>Sterna hirundo</i>
<i>Emberiza citrinella</i>	<i>Sterna paradisaea</i>
<i>Emberiza hortulana</i>	<i>Sternula albifrons</i>
<i>Emberiza melanocephala</i>	<i>Streptopelia decaocto</i>
<i>Emberiza pusilla</i>	<i>Streptopelia turtur</i>
<i>Emberiza rustica</i>	<i>Strix aluco</i>
<i>Emberiza schoeniclus</i>	<i>Strix nebulosa</i>
<i>Eremophila alpestris</i>	<i>Strix uralensis</i>
<i>Erithacus rubecula</i>	<i>Sturnus unicolor</i>
<i>Eudromias morinellus</i>	<i>Sturnus vulgaris</i>
<i>Falco biarmicus</i>	<i>Surnia ulula</i>
<i>Falco cherrug</i>	<i>Sylvia atricapilla</i>
<i>Falco columbarius</i>	<i>Sylvia borin</i>
<i>Falco eleonora</i>	<i>Tachybaptus ruficollis</i>
<i>Falco naumanni</i>	<i>Tachymarptis melba</i>
<i>Falco peregrinus</i>	<i>Tadorna ferruginea</i>
<i>Falco rusticolus</i>	<i>Tadorna tadorna</i>
<i>Falco subbuteo</i>	<i>Tarsiger cyanurus</i>
<i>Falco tinnunculus</i>	<i>Tetrao urogallus</i>
<i>Falco vespertinus</i>	<i>Tetrastes bonasia</i>
<i>Ficedula albicollis</i>	<i>Tetrax tetrax</i>
<i>Ficedula hypoleuca</i>	<i>Tichodroma muraria</i>
<i>Ficedula parva</i>	<i>Tringa erythropus</i>

Table B.1 (continued)

<i>Ficedula semitorquata</i>	<i>Tringa glareola</i>
<i>Fringilla coelebs</i>	<i>Tringa nebularia</i>
<i>Fringilla montifringilla</i>	<i>Tringa ochropus</i>
<i>Fulica atra</i>	<i>Tringa stagnatilis</i>
<i>Fulica cristata</i>	<i>Tringa totanus</i>
<i>Galerida cristata</i>	<i>Troglodytes troglodytes</i>
<i>Galerida theklae</i>	<i>Turdus iliacus</i>
<i>Gallinago gallinago</i>	<i>Turdus merula</i>
<i>Gallinago media</i>	<i>Turdus philomelos</i>
<i>Gallinula chloropus</i>	<i>Turdus pilaris</i>
<i>Garrulus glandarius</i>	<i>Turdus torquatus</i>
<i>Gavia arctica</i>	<i>Turdus viscivorus</i>
<i>Gavia immer</i>	<i>Tyto alba</i>
<i>Gavia stellata</i>	<i>Upupa epops</i>
<i>Gelochelidon nilotica</i>	<i>Vanellus spinosus</i>
<i>Glareola nordmanni</i>	<i>Vanellus vanellus</i>
<i>Glareola pratincola</i>	<i>Xenus cinereus</i>
<i>Glaucidium passerinum</i>	<i>Zapornia parva</i>
<i>Grus grus</i>	<i>Zapornia pusilla</i>
<i>Gypaetus barbatus</i>	

B.2 Model diagnostic plots

The Q-Q plots, residuals vs. fitted plots, histograms of the residuals, and residuals vs. explanatory variables plots for the selected taxonomic and functional stability models are given below.

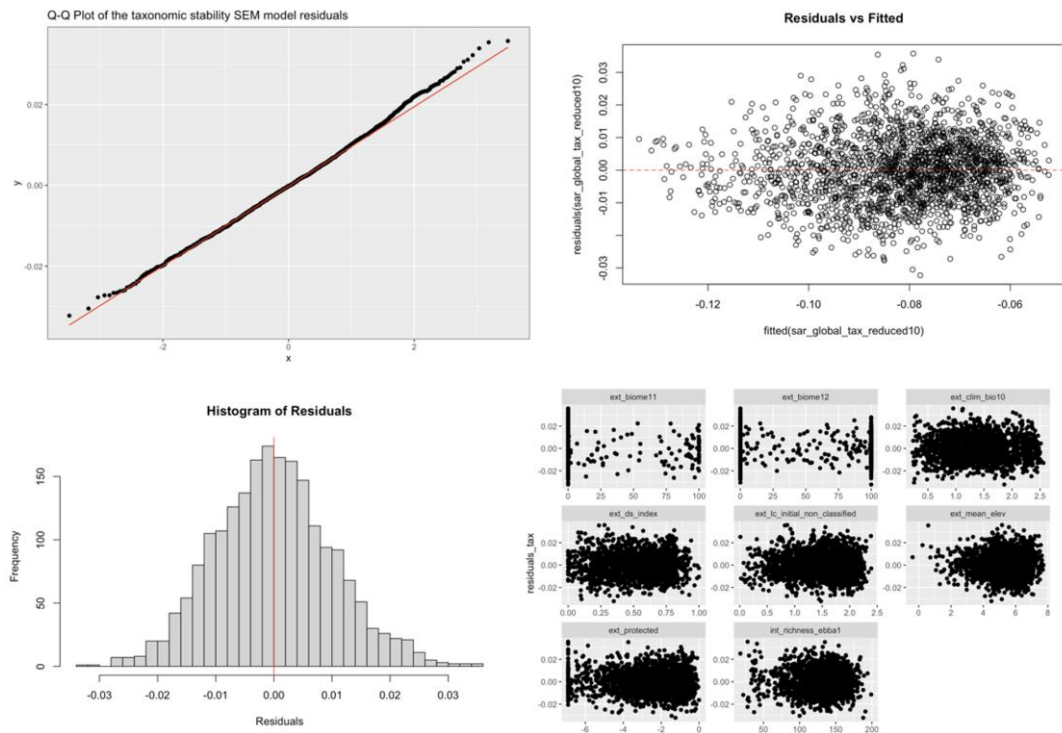


Figure B.1 Diagnostic plots of the final taxonomic stability spatial error model.

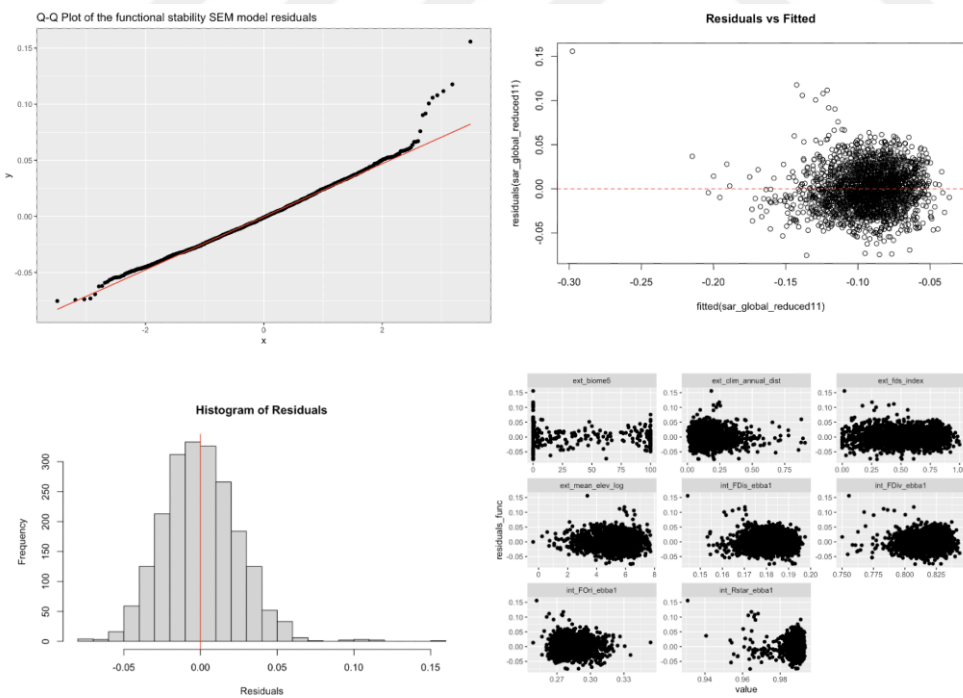


Figure B.2 Diagnostic plots of the final functional stability spatial error model.

B.3 The discussion of the statistical approaches

I used spatial error models (SEM) to test the effects of a wide range of variables on taxonomic and functional stability while accounting for spatial autocorrelation (SAC). Significant SAC in model residuals when I employed generalized linear mixed effect models and generalized additive models (section 2.2.10). I was unable to address the SAC issue by using standard procedures, such as including additional spatial terms in the models (e.g., the country variable), incorporating spatial smooths in generalized additive models, or using Morgan eigenvectors as predictors in linear or non-linear models (Kissling and Carl 2008, Wood 2017). As a result, using beta regression was not a viable option for me, although it would have been the most optimal one.

SEM models require that residuals follow a normal distribution (Anselin 1988, LeSage 2008). However, the response variables analyzed in this chapter (taxonomic and functional stability) are naturally constrained within the $[0, 1]$ range (section 2.2.8), leading to skewed distributions that cause model residuals consistently violate the normality assumption when raw response variables were used (see Figure 2.21 in section 2.2.10). I tackled this issue by transforming the response variables using Box-Cox transformation (Osborne 2010). This approach has previously been employed in ecological research (e.g., da Silva et al., 2012; Legendre & Borcard, 2018), and is justifiable if it effectively resolves issues of non-normality or homoscedasticity (Atkinson et al. 2021). Furthermore, it also preserves as much of the original data structure as possible (Osborne 2010).

For these reasons, I opted to transform the response variables and conducted my analyses using the transformed response variables. While Box-Cox transforming response variables is perfectly okay from a statistical point of view (Legendre and Borcard 2018, Atkinson et al. 2021), the results presented in this chapter should be interpreted with this methodological consideration in mind.

I utilized the k -nearest neighbor approach to define the neighbor structure in the SEM models (Anselin 2002, Getis and Aldstadt 2004). Upon choosing the optimal number of neighbors using an intricate selection procedure described in section 2.2.10.1.1, I ended up with two separate spatial components, which were Iceland and rest of the study area (see Figure 2.3 in section 2.2.1.1 for a map of the study area). This indicated that the study area is made up of two subunits that do not spatially affect one another. Here, having two spatial components in the analysis is not problematic; rather, it reflects the true geographic separation of the regions and ensures that the spatial structure aligns with ecological and biogeographical realities (Getis and Aldstadt 2004). The independence of Iceland in terms of spatial autocorrelation is expected, as it is an isolated island with no direct spatial interactions with rest of the study area. Similar methodological approaches have been applied in biogeographical studies and macroecological analyses, where distinct landmasses are modeled as separate spatial components, with each component maintaining its internal spatial dependence (LeSage 2008, Fotheringham and Rogerson 2013).

I chose to use backward selection as the method of model selection to identify the most influential sets of covariates for each of the two models. This method offers several advantages over other model selection methods. First, backward selection begins with a full model that includes all variables, which minimizes the risk of leaving out an influential variable during the selection procedure (Harrell 2015). Second, it handles collinearity more effectively than the other model selection strategies, such as the forward selection, because one can check for multicollinearity in the global model, reducing the risk of including redundant variables (James et al. 2013). Third, it often results in selection of a more parsimonious model with fewer terms included, leading to a more interpretable model with a reduced the risk of overfitting (Burnham and Anderson 2002). Fourth, compared to exhaustive model selection procedures, such as all-subsets regression using the *dredge* function from the *MuMIn* package (Barton and Barton 2015), backward selection offers a more feasible option for model selection with computationally demanding modeling approaches like SEMs (Bivand 2008, Hastie et al. 2009). Considering these

advantages as well as the size of the dataset and the large number of explanatory variables included in the models (section 2.2.9), backward selection was a logical and appropriate choice for model selection.

B.4 The discussion of the trait-weighting and dimensionality reduction

In this chapter, I used the most recent methods for weighting functional traits prior to functional diversity calculations – the *gawdis* method (de Bello et al. 2021a) – and for assessing the quality of dimensionality reduction, namely the AUC (Mouillot et al. 2021) and mad methods (Magneville et al. 2022).

The *gawdis* approach uses an algorithm to determine the optimal weights for individual traits, ensuring each trait contributes nearly equally to overall trait dissimilarity (de Bello et al. 2021a). This means that a trait that effectively resolves species is downweighted, while a trait with poor resolving power is upweighted. By doing so, the method provides an objective way to assign weights to traits, eliminating the subjectivity involved in manually assigning weights based on trait categories (Petchey and Gaston 2006).

However, one potential drawback is that some researchers may not prefer to downweight a naturally influential trait because of its ecological relevance. Similarly, one might not prefer to increase the weight of a trait that naturally does not have much variance among the studied species. Nevertheless, the *gawdis* approach ensures a nearly equal representation of all traits in the diversity calculations, which is often preferable to these alternative scenarios. Additionally, in my case, the pairwise functional distance matrices generated using the *gawdis* and subjective methods were highly correlated (ρ : 0.95 in Mantel's test) when trait categories or groups were defined (see section 2.2.6). This indicates that the *gawdis* method did not substantially alter trait weights compared to subjective assignment but likely made small adjustments to ensure more balanced contributions from individual traits and trait groups.

The assessment of the quality of the reduced functional space using the AUC and mad (Mouillot et al. 2021, Magneville et al. 2022), along with the percent variation explained criteria, suggested a highly successful representation of the original functional space. However, according to two specific the criteria, namely the AUC > 0.70 and mad criteria (section 2.2.7), my choice of using the first five PCoA axes was suboptimal. Unfortunately, I was unable to include more than five axes in my analyses due to computational limitations, as it was impossible to calculate functional beta diversity beyond 5D space with my large dataset (Baselga and Orme 2012). Fortunately, the mad difference between the most optimal reduction and the 5D representation was only 15%, indicating just a 15% increase in deviation in absolute pairwise functional distances (see Figure 2.14 in section 2.2.7). Given this minor difference, along with the fact that the reduction I employed easily surpassed one of the criterion, the AUC elbow inflection point (Mouillot et al. 2021), and achieved an impressive 94% variation explained, I believe that using the first five PCoA dimensions was a sufficiently optimal choice for my analyses.

B.5 Species with the highest numbers of colonizations and extinctions

Top 10 species with the highest numbers of colonizations and extinctions are presented in Table B.2.

Table B.2 Top 10 species with the highest numbers of colonization (left) and extinction (right) events during the study period.

Colonizations		Extinctions	
<i>Falco peregrinus</i>	689	<i>Lanius excubitor/meridionalis</i>	542
<i>Phalacrocorax carbo</i>	590	<i>Emberiza hortulana</i>	345
<i>Haliaeetus albicilla</i>	589	<i>Circus cyaneus</i>	321
<i>Mareca strepera</i>	533	<i>Actitis hypoleucos</i>	288
<i>Anser anser</i>	472	<i>Galerida cristata</i>	277
<i>Merops apiaster</i>	405	<i>Porzana porzana</i>	262
<i>Cygnus olor</i>	373	<i>Coracias garrulus</i>	254
<i>Panurus biarmicus</i>	368	<i>Calidris pugnax</i>	252
<i>Ardea alba</i>	346	<i>Spatula querquedula</i>	230
<i>Ardea cinerea</i>	336	<i>Asio flammeus</i>	229



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MS	METU Biological Sciences, Biology	2017
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1. Changes in functional composition and diversity of waterbirds: The roles of water level and submerged macrophytes. Özgencil et al., (2020). Freshwater Biology. <https://doi.org/10.1111/fwb.13531>.
2. Update on the status of White-headed Duck *Oxyura leucocephala* and its breeding phenology in Central Anatolia, Turkey. Özgencil and Uslu, (2021). Sandgrouse.
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