# Introduction

## The ecological niche

Every species has requirements to persist in an environment. When these requirements are not met, and without sufficient immigration, populations are destined to local extinctions. This concept of environmental requirements is at the core of the ecological niche, defined as the biotic and abiotic factors for which a species has a positive growth rate and the impact of the species on these factors (Chase & Leibold 2003; Holt 2009). The ecological niche thus encompass species response to and its role within its environment, serving as a central concept for addressing some of ecology’s most fundamental questions: Why are species found where they are? How do so many species coexist? Why are some species rare and others common? How do species interact with one another? What roles do species play in ecosystems? And, crucially, how will species and communities respond to rapid environmental changes?

The theory of the ecological niche emerged from ideas first introduced by Joseph Grinnell and Charles Elton. On the one hand, Grinnell (1917) emphasized species relationships with abiotic factors in his seminal work on the distribution of the California Trasher. He went further, stating that “[..] no two species regularly established in a single fauna have precisely the same niche relationships”, formulating the competitive exclusion principle later predicted by Vito Volterra’s (1928) mathematical models and demonstrated in lab experiments by Georgy Gause (1934). In contrast, Elton (1927) focused on the position of species within its biotic environment, defining the niche as the “status of the animal in the community”. These two perspective set the stage for G. Evelyn Hutchinson to develop his hypervolume model of the niche (Hutchinson 1957). For Hutchinson, the niche is the location where a species can establish and persist in a n-dimensional space where axes are environmental variables. His framework successfully integrate the Grinnellian dimensions of the niche (environmental requirements) in an intuitive quantitative framework, shaping the theoretical work in coexistence (Chesson 2000; Letten *et al.* 2017) and biogeography (Godsoe *et al.* 2017; Guisan & Zimmermann 2000) for decades.

However, the dynamic nature of Eltonian’s dimensions of the niche (relationships to other species) posed challenges in integrating them into Hutchinson’s hypervolume framework (McInerny & Etienne 2012). So, recent research has focused on integrating the Grinnellian and Eltonian niches to better understand the distributions of species (Soberón 2007) and interactions (Gravel *et al.* 2019). This integration raised new questions such as the signature of interactions on species distributions across scales. Traditionally, it was believed that species interactions primarily influence distributions at local scales, while climate shape regional and geographic scale distributions (Pearson & Dawson 2003; Soberón 2007; Whittaker *et al.* 2001). However, there are now evidence that the effects of local species interactions can scale-up to influence distributions at all scales (Araújo & Rozenfeld 2014; Belmaker *et al.* 2015). Although the importance of interactions at larger scale remains debated, it highlights how different niche axes contribute in shaping ecological communities.

Of course, neutral processes also influence communities. First proposed by Hubbell (2001), neutral theory posits that biodiversity is structured in space and time not by ecological differences among species (growth, death, dispersion rates) but by stochastic elements (ecological drift). Despite the unrealistic assumption of perfect equivalence among species, neutral theory successfully predicts many community properties (Bell & Schluter 2000; Canard *et al.* 2012). Modern ecological theories now recognized both niche and neutral processes as central to shaping ecological communities (Vellend 2010), and playing crucial roles in explaining ecological succession, dynamics and interactions (Gravel *et al.* 2006; Morales-Castilla *et al.* 2015; Poisot *et al.* 2015).

## Biogeography

One of the subfield of ecology most profoundly influenced by niche theory is biogeography, the study of how biodiversity is distributed. Based on the niche framework, species distribution models brought biogeography from a mainly descriptive science to a science that provides testable predictions (Elith & Leathwick 2009; Pulliam 2000). Correlative species distribution models quantify species niches by relating observed species occurrences to environmental variables (Elith & Leathwick 2009). However, the true relationship between species niche and what species distribution models describe is unclear. While they depend on observations of the realization of species niches (Booth *et al.* 1988), most species distribution models fail to account for other factors influencing species distribution such as biotic interactions and dispersal limitations (Araújo & Guisan 2006; Godsoe *et al.* 2017). This deficiency has been one of the main critique of species distribution models, particularly for spatial and temporal extrapolation (Thuiller et al. 2013; Urban et al. 2016; Zurell et al. 2009). Efforts have been made to integrate dispersal limitations and biotic interactions directly or indirectly into models, although implementation remains challenging due to data constraints (Engler & Guisan 2009; Pollock *et al.* 2014; Shipley *et al.* 2022; Staniczenko *et al.* 2017). Despite these limitations, species distribution models have proven indispensable in elucidating spatial and temporal patterns, bridging knowledge gaps, and emerging as a vital conservation tool (Guisan *et al.* 2013; Pollock *et al.* 2020).

The history of biogeography can be traced back to the work of Alexander von Humboldt. In his 1807 essay, Humboldt noted how plant communities tend to be more diverse as one move closer to the equator (Humboldt *et al.* 2008). Mechanisms explaining this latitudinal gradient of diversity would be proposed only centuries after Humboldt’s work and remains heavily debated (Mittelbach *et al.* 2007; Pianka 1966). Another key figure in the foundation of biogeography is Alfred Russel Wallace. During his extensive travels in the mid-19th century, Wallace noticed that how vertebrate families are distributed tend to form distinct geographical units. Based on this observation and on the existing knowledge of his time, he proposed that the Earth's land surface can be divided in zoogeographic regions based on species distributions (Holt *et al.* 2013; Wallace 2011). These two seminal work paved the way for the exploration of other generalities and peculiarities of how the diversity of life distributes in space and time, such as the relationship between diversity and area (Preston 1960) or the work on island biogeography (MacArthur & Wilson 2001). Understanding how these patterns emerge have been among the most fruitful avenue to enhance our understanding of how communities assemble, persist and function.

Some biogeographic patterns are so widespread that they have been designated as ecogeographic “rules”. One of these rules is the latitudinal diversity gradient, the same decrease in species diversity towards the poles that Humboldt noted (Hillebrand 2004). Various explanations have been proposed for this gradient, including the effects of higher productivity and climate stability in the tropics on speciation rates, niche partitioning, specialization, and biotic interactions (Mittelbach *et al.* 2007; Pontarp *et al.* 2019). Another gradient of longstanding interest is the relationship between body mass and temperature. Originally proposed by Bergmann (1848), the rule is traditionally defined as ‘races of warm blooded vertebrates from cooler climates tend to be larger than races of the same species from warmer climates’ (Mayr 1956). While the exact reasons for this gradient's emergence are still debated, it is generally believed that larger-bodied animals possess better heat retention, enabling them to thrive in colder environments compared to smaller individuals (Blackburn *et al.* 1999). This principle has been extended to encompass the relationship between size and latitude for ectotherms and across closely related species, as originally proposed by Bergmann (Blackburn et al., 1999).

A recent development in biogeography is expanding focus from solely considering the distribution of organisms to trying to understand distribution of interactions and the ecological network they form (Windsor *et al.* 2023). Interaction networks can vary through two main processes: (1) changes in community composition, and (2) changes in the functional relationships between interacting species, like the body mass ratio between predators and prey (Poisot *et al.* 2015). These two processes are, in turn, influenced by factors such as the environment (Pellissier *et al.* 2018), the regional pool of interactions (Saravia *et al.* 2022), area (Galiana *et al.* 2018), or higher-order interactions (Poisot *et al.* 2015). Based on previous knowledge on species biogeography and on how species interaction network are structured, it is possible to formulate predictions regarding how network properties vary across space and scale (e.g., Baiser et al. 2019; Gravel et al. 2011) but the empirical investigation on these patterns are still rare (e.g., Baiser et al. 2012; Galiana et al. 2021; Gravel et al. 2019; O’Connor et al. 2020).

## Relations between species traits and niche

Species functional traits are morphological, physiological or phenological characteristics of a species that influences its performance (growth, survival, reproduction) in an environment (Violle *et al.* 2007). These traits evolved in response to environmental conditions and interactions with other species (Reich *et al.* 2003). Although the concept of functional trait have originally been developed for plant ecology (Funk *et al.* 2017), there is ample evidence of functional traits relevant to animal responses to (Vandewalle *et al.* 2010) and their impact on (e.g., Lundgren et al. 2024) their environment. Therefore, functional traits are directly related to species niches (McGill *et al.* 2006) providing insights into the role of niche differentiation and environmental filtering in species distributions and community assembly (Zakharova et al. 2019). For example, Lamanna et al., (2014) showed how quantifying the volume, packing, and overlap of functional trait space across scales could test different hypotheses for the latitudinal gradient in species richness. A clear benefit of traits is that, unlike species niches, they can be directly measured, providing a accessible quantitative framework for prediction (Kearney *et al.* 2010).

Given that species with similar traits are expected to show similar responses to the environment, traits hold promise for improving predictions of species distributions and anticipating responses to environmental changes. For example, using a hierarchical species distribution model, Pollock et al. (2012) showed how Eucalypt species’ leaf area, plant height, and seed mass influenced species response to environmental gradients. Not only do these trait-based predictions provide a more mechanistic understanding of how traits influence species distributions, but they have been shown to also help model transfer across species and space (Vesk *et al.* 2021). Functional traits can also predict species vulnerability to global warming (Pacifici *et al.* 2017) and precipitation regimes (Griffin-Nolan *et al.* 2018). Thus, trait-based predictions serve as valuable tools for filling gaps in our understanding of species and ecosystems' distributions and responses to abiotic factors, particularly for those about which we have limited knowledge.

Species sharing traits should also share similar interactions. For example, in a study looking at all predator-prey interactions for European vertebrates, O’Connor et al. (2020) found that species traits strongly explained species trophic groups (species sharing similar resources and enemies). Therefore, traits also provide a framework to predict interactions (Bartomeus *et al.* 2016; Gravel *et al.* 2013). For trophic interactions, this means that the traits (e.g., body mass, activity time, foraging strata) of predators should determine the type of species it can feed on. Similarly, the traits of the prey should determine the type of predator a species has. These assumptions are encompassed in ‘trait-matching’ models that aim to predict functionally feasible interactions within a species pool (Morales-Castilla *et al.* 2015). Thes trait-matching models have been shown to predict accurately potential species interactions for a number of ecosystems, taxa, and interaction types (Brousseau *et al.* 2018; Laigle *et al.* 2018; Pichler *et al.* 2020; Pomeranz *et al.* 2019). Once again, these trait-based models offer a promising avenue for gaining a mechanistic understanding of how traits relate to niches and for filling knowledge gaps regarding species interactions (Hortal *et al.* 2015).

## Trophic interactions and food webs

Trophic interactions, where a predator species feed on a prey species, constitute one type of species interactions. The collection of these trophic interactions among species form a food web, a fundamental concept in ecology to understand ecosystem structure and dynamics (Lindeman 1942; Thompson *et al.* 2012). The identity, strength and organization of trophic interactions influence how species distribute in space (Wisz *et al.* 2013), how populations respond to disturbances (Eklöf & Ebenman 2006), and how energy flow within and between ecosystems (Gounand *et al.* 2018). Given that food webs integrate biodiversity and ecosystem function, conserving their structure and the underlying trophic interactions is essential to protect the diversity and integrity of ecosystems (Harvey *et al.* 2017). For example, investigating the position of a species within a food web inform on its role within the community and help anticipate secondary extinction (Cirtwill *et al.* 2018; McDonald-Madden *et al.* 2016).

Food webs have emerging properties with important implications on the communities, such as the level of connectivity (connectance), the structure of specialization among species, or the formation of modules (Delmas *et al.* 2019; Pimm *et al.* 1991). May famously showed that under random interaction networks, a more complex food web (measured by level of connectance, species richness, and mean interaction strength) should be less stable, challenging the commonly accepted assumption of the time that more complex systems are more stable (May 1972). This insight inspired decades of research aimed at understanding how observed properties of empirical food webs, such as the organization of interactions, the distribution of interaction strengths or the correlation between interspecific interactions, influence the relationship between complexity and stability (Allesina & Tang 2015). Another example of how food web structure influences communities is demonstrated by network complementarity, where species partition resources and enemies, leading to increased ecosystem productivity (Poisot *et al.* 2013). Thus, it is not only the number and identity of trophic interactions that matters, but also how they are organized among species.

Yet, we still face major challenges when developing accurate descriptions of natural food webs and apply our theoretical understanding of food webs to conservation. One major obstacle is the lack of trophic interaction data across most locations and taxa (Poisot *et al.* 2021), which presents fundamental technical and practical challenges in food web ecology. In fact, the “lack of knowledge about interactions among species or among groups of species” remains one of the major biodiversity data shortfalls (Hortal *et al.* 2015). Sampling interactions is inherently difficult; observing an interaction requires simultaneously detecting individuals of two species while they are interacting. It is virtually impossible to sample all interactions even for a simple community and large sampling effort (Chacoff *et al.* 2012; Jordano 2016; Pringle & Hutchinson 2020). Additionally, there are spatial biases in available food web datasets, with a disproportionate focus on the United States and Europe (Cameron *et al.* 2019; Poisot *et al.* 2021). These biases collectively limit the scale of food web research and pose significant hurdles to the necessary shift in focus from species to interaction networks in conservation efforts (Harvey *et al.* 2017).

To address these gaps, models have been developed to predict trophic interactions based on food web theory (Strydom *et al.* 2021). Both neutral and niche processes determine which two species will interact (Morales-Castilla *et al.* 2015). Neutral models of species interactions predict that feasible interactions are only dependent on species presences and abundances (Canard *et al.* 2012). The interactions that do not occur under this constraint are termed neutrally forbidden interactions (Morales-Castilla *et al.* 2015). Although neutral models can predict a significant amount of variation in interaction strengths (Canard *et al.* 2014), recent research has highlighted that co-occurrences do not always imply interaction (Blanchet *et al.* 2020; Thurman *et al.* 2019). In contrast to the neutral model, niche-based models predict that interactions between two species depend on their respective traits (Rossberg *et al.* 2010). Non-interactions driven by niche-based processes are termed functionally forbidden interactions (Morales-Castilla *et al.* 2015), and can be predicted by trait-based models of interactions (Bartomeus *et al.* 2016). Phylogenetic relationships also provide valuable information, serving as proxies for trait relationships, and because interactions and species' roles (i.e. species' positions in the food web) tend to be evolutionarily conserved (Gómez *et al.* 2010; Stouffer *et al.* 2012).

At the network level, factors beyond those acting at the interaction level (neutral and niche processes) also constrain food webs. Firstly, local interactions are drawn from the pool of interactions at the regional scale, thus local food webs are constrained by the regional web of interactions, often referred to as the regional metaweb. Recently, Saravia et al. (2022) showed that properties of food webs emerge from the metaweb, suggesting that the regional food web structure is primarily constrains local food web structure. Secondly, there are evidence that the environment influences the local realization of food webs. For example, primary productivity should determine the number of trophic levels and number of species at each trophic level an ecosystem can sustain (Thompson & Townsend 2005). Additionally, area have also been showed to influence the shape of the food webs (Galiana *et al.* 2018). Spatial (e.g., habitat diversity) and temporal (e.g., seasonality) factors are also believed to shape modules within network (McMeans *et al.* 2015; Rooney *et al.* 2008). For example, species occurring in the same habitat type or season will form highly connected module relative to species not present at the same time or space. Finally, there are dynamic constraints on the local realization of food webs (Grilli *et al.* 2017). Theory predicts that for a food web to be persist, it needs to lead to a feasible and stable equilibrium. In short, food webs are a product of neutral and niche constraints acting at the level of interactions, as well as neutral, environmental, and dynamic constraints at the network level.

## Bird niche and threats across seasons

Migratory species are facing significant declines worldwide (Bairlein 2016; Studds *et al.* 2017; Wilcove & Wikelski 2008). For example, Rosenberg et al. (2019) estimated a 29% decrease in North American bird abundance between 1970 and 2019. To mitigate this decline, we need a comprehensive understanding of bird ecology and stressors over their full annual cycle and protect their entire migratory network (Marra *et al.* 2015; Xu *et al.* 2020). Stressors impacting individuals in one season can carry-over to affect the survival and reproductive success at other seasons (Norris *et al.* 2004; Reudink *et al.* 2009). Despite the importance of a year-around understanding, most studies historically focused on a single season, usually the growing season (Marra *et al.* 2015). For effective conservation efforts, it is imperative to gain a deeper understanding of bird distribution, threats, environmental responses, and interactions throughout the entire year.

Migration is though to have evolved in response to seasonality, allowing species to maintain fidelity to favorable breeding grounds while escaping harsh conditions (Winger *et al.* 2019). Unlike other adaptation to seasonality such as hibernation or freeze tolerance, migration allows species to maintain consistent thermal conditions throughout the year but comes with movement costs (Gómez *et al.* 2016; Nakazawa *et al.* 2004). Indeed, Somveille et al. (2015, 2019) showed that breeding and wintering destinations of migratory birds are optimized to avoid unfavorable climatic conditions, competition, and minimize travel distance. Therefore, evidence suggests there is a fundamental trade-off between the movement within geographic and climatic niche spaces (Gómez et al., 2016; Nakazawa et al., 2004), but it is poorly understood how the differences between species alter the balance of this trade-off.

Species' strategies for minimizing movement within their climatic niche space versus enduring variation in climatic conditions are influenced by geographic, morphological, life history, predatory, and feeding habits (Cohen & Jetz 2022; McKinnon *et al.* 2010; Zurell *et al.* 2018). For example, larger species should be more likely to minimize travel distance has they usually need more energy to migrate (Watanabe 2016) and can tolerate colder temperatures (Blackburn *et al.* 1999). Similarly, species with a flexible diet, like the Northern cardinal (*Cardinalis cardinalis)*, which switches from feeding on insects and berries in summer to a mainly granivorous diet in winter (Gill 2007), are less likely to migrate to track resources. While these examples illustrate how certain traits explain why some birds favour movement within climatic space over movement in geographic space, we are still lacking evidence for the influence of other traits.

Understanding how traits influence how species' balance the trade-off between geographic and within-niche movements can provide a more mechanistic insight into the significant seasonal shifts in diversity highlighted in recent literature. For example, Ng et al. (2022) observed seasonal variations in the biomass, abundance, and richness of nocturnal migratory landbirds in the United States, with higher abundance and diversity in the Southeast and Pacific coast during winter, and in the Northeastern and Midwestern United States during summer. Similarly, La Sorte et al. (2022) noted that bird richness peaked on islands in the northern mid-latitudes during migration, shifting to tropical latitudes in winter. Additionally, the functional composition of bird assemblages varies seasonally, as demonstrated by Jarzyna & Stagge (2023), who found that functional richness is highest in winter despite a decrease in species richness in the Northeastern United States. These findings underscore a strong functional basis for seasonal diversity patterns, yet the specific traits driving major diversity gradients remain incompletely understood.

As migratory birds change their ranges between seasons, so are the level of protection and the threats they experience. Runge et al. (2015) showed that globally, only 9% of 1451 migratory birds are adequately covered by protected areas across all stages of their annual cycle, compared with 45% for nonmigratory birds. Most Important Bird and Biodiversity Areas, which serve as the basis for bird site-based protection worldwide, are identified in the bird’s breeding distributions. Therefore, it is not surprising that protection of migrating routes are often incompletely protected. Yet, the importance of adequate protection of the entire migratory network has been demonstrated and proposed as key in slowing down the decline of migratory species (Marra *et al.* 2015; Runge *et al.* 2015; Wilcove & Wikelski 2008; Xu *et al.* 2020; Zhang *et al.* 2023). Birds also experience different level of stress throughout their annual cycle. For example, La Sorte *et al.* (2022) recently showed that exposure to air pollution differ between seasons for world’s nocturnally migrating birds, and that this exposure will also change differently among seasons in the future. For effective conservation efforts, it is imperative to gain a deeper understanding of the level of protection and threats among bird species and how they are associated with the observed trends in abundances.

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