

Review

Using multi-scale spatially explicit frameworks to understand the relationship between functional diversity and species richness

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Understanding how ecosystem functioning is impacted by global change drivers is a central topic in ecology and conservation science. We need to assess not only how environmental change affects species richness, but also how the distribution of functional traits (i.e. functional diversity) mediate the relationship between species richness and ecosystem functioning. However, most evidence about the capacity of functional diversity to explain ecosystem functioning has been developed from studies conducted at a single spatial scale. Here, we explore theory, expectations and evidence for why and how species richness and functional diversity relationships vary with spatial scale. Despite the importance of accounting for spatial processes at multiple scales, we show that most studies of the species richness–functional diversity relationship focus on single scale analyses that ignore spatial context. Thus, we discuss the need to establish a spatially explicit, multi-scale framework for understanding the relationship between species richness and functional diversity. As a starting point to developing such a framework, we detail some expected trajectories and mechanisms by which the diversity of species and functional traits may change across increasing spatial scales. We also explore what is known about two important gaps in the literature about this relationship: 1) the influence of spatial autocorrelation on community assembly processes and 2) the variation in the structure of species interactions across spatial extents. We present some key challenges that could be addressed by integrating approaches from community and landscape ecology. This information will help improve our understanding of the relative influence of local and large-scale processes on community structure, while providing a foundation for improving biodiversity monitoring, policy and ecosystem function based conservation.

Keywords: disturbance, ecosystem functioning, functional divergence, functional evenness, functional richness, interaction networks



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Introduction

A central topic in ecology and conservation science consists of improving our understanding of how species diversity is related to ecosystem functioning (Hooper et al. 2005, Díaz et al. 2007, Tilman et al. 2014, Gross et al. 2017). Extensive evidence suggests that patterns of species richness tell us relatively little about the ability of species assemblages to provide specific ecosystem functions, especially in systems heavily impacted by anthropogenic changes such as habitat fragmentation and degradation (de Bello et al. 2010, Mayfield et al. 2010). Functional trait diversity (hereafter functional diversity), defined here as the variation and dispersion of functional traits represented in the species making up a biological community (Mason et al. 2005, Petchey and Gaston 2006), is considered to be a good proxy for how species interact with the environment and contribute to ecosystem functioning (Cadotte et al. 2011, Lavorel et al. 2013). Although trait-based studies are not directly comparable to biodiversity ecosystem functioning studies, it is generally assumed that ecosystems with high functional diversity have higher overall 'functionality' (Lavorel et al. 2013). Therefore, metrics of functional diversity have been used to evaluate species responses to environmental change, as well as the effect of species on ecosystem functions such as nutrient cycling, pollination and primary productivity (Mori et al. 2013, Bu et al. 2019, Woodcock et al. 2019). Evaluating the relationship between species richness and functional diversity is thus important to understand how to preserve multiple components of biodiversity in multifunctional landscapes.

Most of our understanding of the capacity of functional diversity to explain ecosystem functioning has been developed as an extension of theory on fine (or single) spatial scale ecological systems (Mason and de Bello 2013, Gonzalez et al. 2020). While it is clear that relationships between functional diversity and spatial scale are often more complex than species–area relationships and depend on the metric analysed (de Bello et al. 2013a, Smith et al. 2013, Jarzyna and Jetz 2018, Zhang et al. 2018), questions remain about what broad expectations can be drawn about this relationship. What we do know largely reflects outcomes of studies of particular scenarios rather than a generally applicable theoretical framework, and the overall theoretical expectation for how functional diversity is expected to change with spatial scale remains confusing. Therefore, there is a need to synthesizing evidence about the effect of processes acting at multiple scales on the relationship between functional diversity and species richness.

Among the many factors that affect species richness and functional diversity, two are key in shaping communities across spatial scales. These factors are the influence of the spatial distribution of environmental filters on community assembly (de Bello et al. 2013b, Biswas et al. 2016, Chalmandrier et al. 2017), and the variation in the structure of species interactions across spatial extents (Montoya et al. 2015, Galiana et al. 2018). Environmental filters such as disturbance and soil types alter the spatial distribution of

resources and this is reflected in the type of species that are able to colonize and survive in a particular site (Biswas et al. 2017, Brice et al. 2016). For example, an increase in disturbance can create heterogeneous habitats with a high variation in environmental conditions in spatially adjacent locations. This increase in heterogeneity may lead to opportunities for species with different requirements to coexist, thus reflecting significant trait divergence at site (Gross et al. 2013, Cappelatti et al. 2020) and landscape scales (Mendes et al. 2016). Once species overcome the dispersal barrier and fit the environmental conditions of a given site, species interactions then determine which species can integrate a community (as per community assembly theory, see HilleRisLambers et al. 2012 for an extensive review on this topic). Biotic interactions, such as the exclusion of weaker competitors, may cause strong trait convergence in areas with a homogeneous distribution of resources, resulting in a bias towards traits associated with strong competitive ability (Mayfield and Levine 2010, Chalmandrier et al. 2013). On the other hand, biotic interactions can lead to high levels of functional diversity if environmental conditions such as high productivity favour trait divergence among species (Laliberte et al. 2013). By understanding the relative influence of species interactions and the spatial distribution of environmental filters on the spatial scaling of functional diversity, we can better predict about when and under what conditions we expect a positive or negative association between functional diversity, species richness and spatial scale (Fig. 1).

Here, we discuss the need to establish a spatially explicit, multi-scale framework for understanding the relationship between species richness and functional diversity. We illustrate some expected mechanisms by which the relationship between species richness and functional traits may change predictably across increasing spatial scales. We also synthesize evidence on two main topics that are currently lacking from existing frameworks and that are integral to multiscale analyses of functional diversity and species richness relationships: 1) the influence of spatial autocorrelation of habitat types on this relationship and 2) the variation in the structure of species interactions across spatial extents. The synthesis presented here offers new insights into ecosystem functioning at spatial scales that are the most relevant to biodiversity conservation and policy. Key definitions of used in this synthesis can be found in the Supporting information.

Variation in functional diversity across spatial scales

Components of spatial scale

Two main components of spatial scale are important to consider in regards to biodiversity–environment relationships (McGarigal et al. 2016): spatial resolution (i.e. grain size) and spatial extent. Spatial resolution corresponds to the plot or sampling size at which communities and environmental attributes are measured, whereas spatial extent is the total

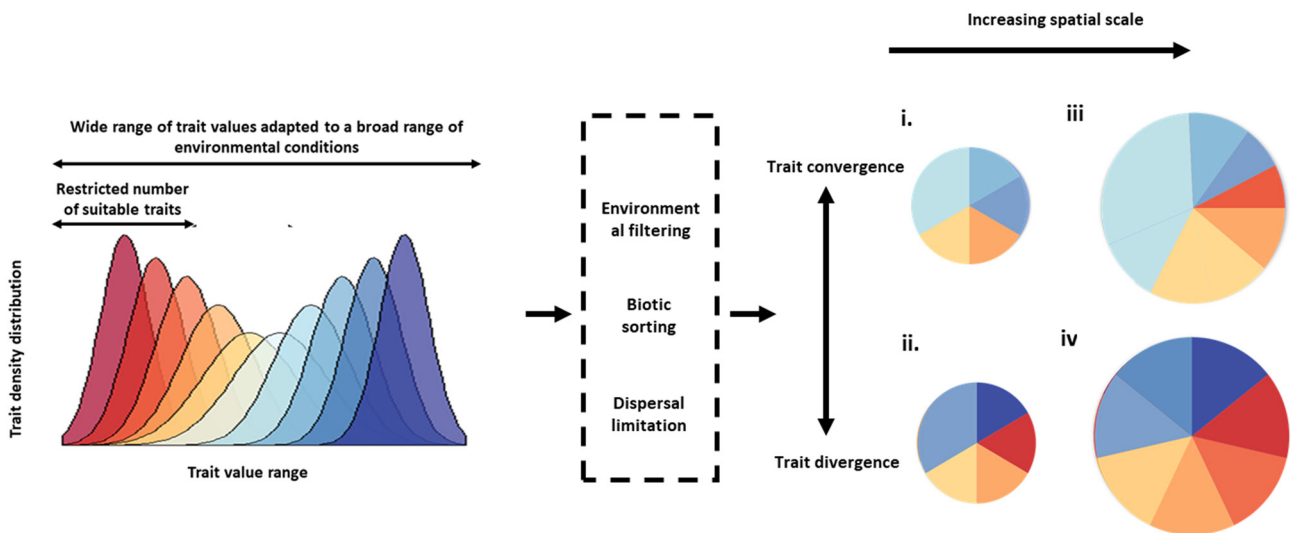


Figure 1. Patterns of trait diversity at multiple spatial scales depend on how the environment filters species based on the trait compatibility with a given environment, as well as on the traits that impact each species' contextual ability to compete for limited resources. We illustrate this showing the trait value distribution for a species pool of ten species. Each density probability distribution corresponds to one species. All species present in each local community on the right have already 'passed' the prevailing environmental and dispersal limitation filters. Biotic interactions such as the exclusion of weaker competitors may cause strong trait convergence at the site or neighbouring scale, where only strong competitive traits are retained (i). On the other hand, factors such as high resource productivity and environmental heterogeneity may lead to significant trait divergence (ii). Pie charts on the right (iii, iv) show potential distribution of trait values for communities sampled at larger scales. iii) Trait convergence increases with spatial extent, iv) Trait divergence increases with spatial extent.

area that encompasses the species pool under consideration. At landscape and regional spatial extents, we expect to find larger species pools composed of species with a diverse set of functional traits adapted to a broad range of environmental conditions found across space (e.g. elevational and climatic gradients) (de Bello et al. 2013b, Yang et al. 2014, Chalmandrier et al. 2017). In contrast, at the site or patch scale, groups of species or individuals are expected to be more restricted in the number of suitable traits present given local conditions (de Bello et al. 2012a, b). Increasing the sampling resolution (smaller grain size) increases the detectability of fine-scale associations between species, traits and local environmental conditions, as well as the types of biotic interactions that are important for species co-existence at local scales (Bergholz et al. 2017). To capture this ecological nuance, data are needed at neighbourhood scales to determine which species are directly competing for which resources. For example, in plant systems, data on fecundity or growth in response to gradients of resource availability (e.g. light and nutrients) between neighbouring plants can be used to parameterize population growth models (Coates et al. 2013). This information can improve our ability to determine which types of biotic interactions occurring at local scales also impact larger scale patterns of trait diversity. However, by focusing on very localised aspects of communities, we can miss details about processes that influence the dispersal of individuals from other populations and operate at coarser resolutions and spatial extents. For example, processes related to edge effects, patch isolation and the degree at which landscape matrix allows the movement of individuals between patches, may be only

evident at landscape and regional extents (Didham et al. 2012, Barbaro et al. 2014, Zambrano et al. 2019). Characterizing functional diversity thus requires a clear definition of the spatial extent and the resolution of analysis.

Although we focus our synthesis on aspects of spatial scale, we recognize that effects of spatial processes are also tied to temporal variability (Saar et al. 2017). It is well understood that changes enacted at local to regional, and even global scales (like climate change) can trigger a response in species diversity that take medium to long time scales to become fully evident (Le Provost et al. 2020). It is worth noting that once an ecosystem is transitioning to a new stage, much ecological theory can no longer be applied to these systems. In these situations, it may be crucial to lean on theory developed for transient systems to better understand how the relationship between species and functional diversity is expected to change in response to environmental changes. Addressing how this relationship is likely to change over temporal scales lies outside the scope of this paper. We thus note that whilst both spatial and temporal scales are likely important, here we focus on spatial dimensions alone.

Components of functional diversity

Functional diversity is a multidimensional concept that can express either the composition of functional traits in a community or the distribution in abundances of trait values across functional trait space (Fig. 2; Villéger et al. 2008, Mouchet et al. 2010). Here, we focus on three key metrics – functional richness, functional evenness and functional

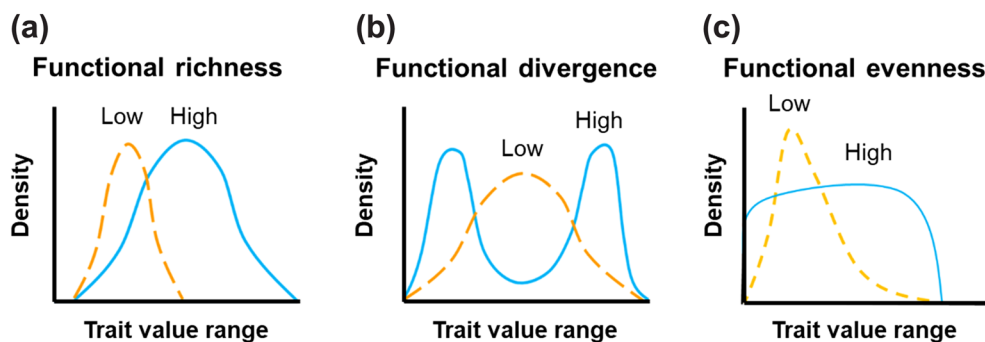


Figure 2. Illustration of the components of functional diversity considered in this review.

divergence – to explain how the diversity of traits likely varies across spatial scales. Functional richness represents the volume filled in trait space by the community of interest (Fig. 2a, Villéger et al. 2008). Functional divergence represents the degree to which the abundance in functional trait space is distributed toward the extremes of its distribution (Fig. 2c). Mathematically, it can be described as the farthest distance, as measured by species abundances, from the centre of the trait space (Carmona et al. 2016). High functional divergence indicates a high degree of niche differentiation, low resource competition and theoretically an increased ecosystem function as a result of more efficient resource use (Mason et al. 2005). Functional evenness describes how uniformly species abundances are distributed in functional space (Mouchet et al. 2010, Carmona et al. 2016), and is highest when all trait values have the same abundances across individuals (Fig. 2c). Below, we explain some of the main mechanisms by which the diversity of species and different metrics of functional diversity are expected to change across spatial scales (Fig. 3). The relationships that we describe should not be considered as an exhaustive list, but rather as a list of outcomes that are expected to be common and that could be tested with studies conducted across regions and ecosystems.

Expected relationships between functional richness and species richness across spatial scales

The relationship between species richness and functional richness depends on the relative influence of environmental filtering and biotic sorting across spatial scales (Smith et al. 2013, Escobedo et al. 2020). At plot (< 100 m²) and patch extents, there are many examples where competition for resources leads to high trait richness compared to expectations from null models (de Bello et al. 2012b, Laliberte et al. 2013, Biswas et al. 2016). Experiments in grasslands have shown that in patches with high productivity and low grazing intensity, competition is likely to be more intense and promotes trait divergence (Laliberte et al. 2013). However, in fusing population coexistence theory with theories of community assembly, Mayfield and Levine (2010) showed that competitive exclusion can sometimes promote species with similar traits. This can happen when a limiting resource (e.g. light) leads to the persistence of specific phenotypes and

filters species with similar resource acquisition strategies (e.g. individuals that grow slowly and are therefore too short to gather enough light early in their life history; Gross et al. 2017, Saar et al. 2017). In this case, low functional richness at site scales might not only be driven by abiotic conditions (e.g. environmental filtering) or disturbance intensity, but by competitive exclusion as well.

Overall, as spatial extent increases, we expect to see a positive relationship between functional richness and species richness, because there are more environmental conditions that promote the sorting of species across environmental gradients (Chalmandrier et al. 2017). In addition, greater environmental heterogeneity at landscape and regional extents will allow higher levels of nestedness (tendency of assemblages to be subsets of one another) and turnover (Jarzyna and Jetz 2018). In unconnected landscapes, species with certain traits (e.g. short dispersers, slow growers) may only be represented within isolated subsets of the environment, which can lead to an increase in functional trait turnover and nestedness as spatial scale increases (Adler et al. 2013, de Bello et al. 2013a, Kraft et al. 2015). For example, nutrient enrichment can limit the type of macroinvertebrate species inhabiting a particular lake. In this case, functional diversity in enriched lakes represent a small subset of functional diversity at the drainage scale (Hill et al. 2019). On the other hand, strong environmental filtering can promote niche convergence, producing lower than expected functional richness in species-rich assemblages. Freschet et al. (2011) demonstrated that although trait variance is highest between biomes and within plant assemblages evaluated at landscape scales, mechanisms of convergence dominated over divergence at regional scales (i.e. between communities). This a pattern was interpreted as a product of environmental filtering owing to the drastic abiotic differences in temperature, soil moisture and fertility between biomes. From a sample of 50 papers analysing the relationship between species richness and functional diversity at different spatial scales (Fig. 4, see Supporting information for methods), we found that even though increases of functional richness are common at landscape and regional extents, around 25% of the studies showed that functional richness does not increase when spatial extent increases. Thus, the relationship between functional richness and species richness is highly dependent on how heterogeneous the environment

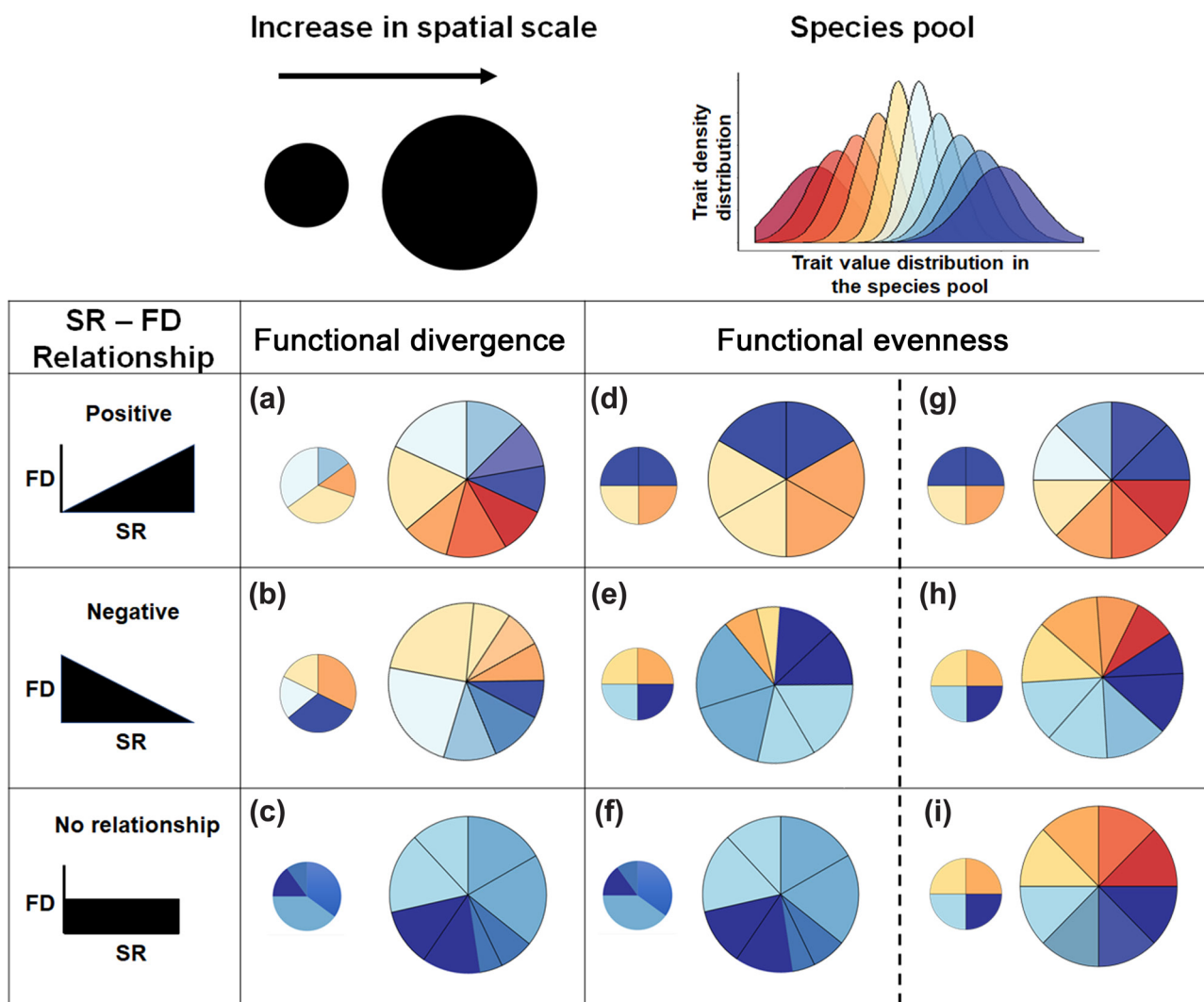


Figure 3. Range of changes in the relationship between functional divergence and species richness (left column) and between functional evenness and species richness (right column) as spatial extent increases. Pie charts show the distribution of different trait values at different spatial extents. Pie subdivisions represent different species, their colour match the trait value distribution in the species pool and their size represent two different spatial extents. Positive relationships between species richness and functional divergence arise when species with extreme trait values are sampled (a), whereas negative relationships represent a convergence towards the mean of the trait value distribution (b). The columns separated by a dotted line show that similar relationships between functional evenness and species richness can arise from contrasting mechanisms. Communities on the right panels have similar levels of functional evenness but higher levels of functional richness compared to communities on the left panels. For example, negative relationships can appear if species with particular traits become dominant, or if species with new trait values that show low abundances are sampled when spatial extent increases. No relationships represent cases where functional diversity remains unchanged as contrasting patterns of trait divergence and convergence occur simultaneously at landscape and regional scales. See further explanation in the text.

is to allow the existence of species with different traits across environmental gradients.

Expected relationships between functional divergence, functional evenness and species richness across spatial scales

Measures of functional diversity that account for the relative abundance of traits tend to show more contrasting responses to spatial scale than functional richness (Karadimou et al. 2016, Yeager et al. 2017). At patch or plot scales, environmental

factors such as disturbance intensity and resource availability can be used to determine which types of species are most likely to dominate (Mayfield and Levine 2010, Shipley 2010). When resource availability is low, species with traits associated with high competitive ability and stress tolerance are more likely to be dominant (Grime 2006, Mayfield and Levine 2010), and thus trait similarity between the most abundant species is expected. This has been shown for multiple systems that have experienced extensive disturbance (Carmona et al. 2015, Karadimou et al. 2016, Rossi et al. 2020). In grassland systems sampled in different sites distributed at regional

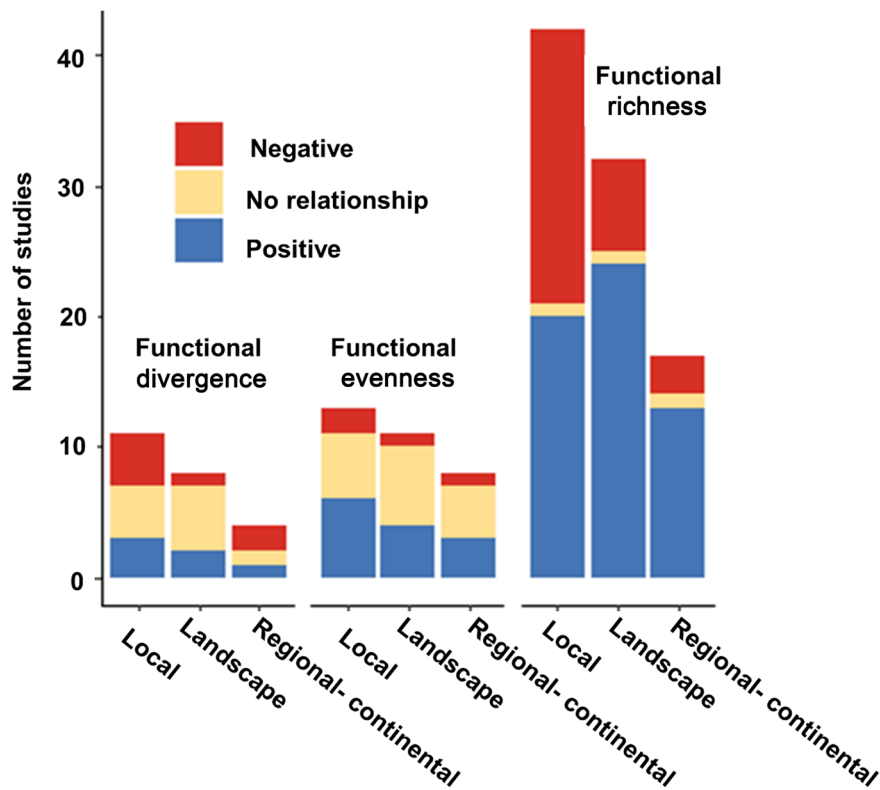


Figure 4. Proportion of studies ($n = 50$) explicitly looking at how the relationship between species richness and functional diversity varies at multiple spatial extents. A negative relationship between functional richness and species richness represents processes of trait convergence where co-existing species tend to express similar trait combinations. For simplicity, we have used three categories of spatial extents: local (plots, patches, sites) landscapes and regions/continents. See definitions in Supporting information.

scales under different levels of disturbance and management intensity, for example, tall, fast growing plants that are good at competing for light tend to exclude other species with less suitable traits, thus favouring low levels of functional evenness and divergence within communities (Gross et al. 2017, Saar et al. 2017). Alternatively, intermediate levels of disturbance can increase environmental heterogeneity and prevent competitive exclusion from occurring at both site and landscape scales, thus favouring the coexistence of functionally dissimilar species (Pakeman 2011, Escobedo et al. 2020). From our review of empirical studies, we found that studies looking at functional divergence and functional evenness at multiple scales are still scarce compared with those looking at the relationship between species richness and functional richness (Fig. 4). However, from those studies evaluating functional divergence and functional evenness (less than 25% of the studies), it is clear that the relationship between species richness and measures of trait abundance across scales is context dependent and can be highly variable across spatial scales.

Expected relationships between functional divergence and species richness across spatial scales

There are multiple mechanisms that can shift the relationship between functional divergence and species richness at different spatial scales. At small scales, processes such as facilitation

(Perronne et al. 2017) and an increase in resource productivity (Ding et al. 2012, de Bello et al. 2013b, Biswas et al. 2016, Escobedo et al. 2020) can prevent exclusion of weaker competitors, promoting trait divergence and increasing species richness. At coarser scales, a heterogeneous distribution of resources and complementarity across environments (Pakeman 2011, de Bello et al. 2013a) can promote higher levels of divergence by supporting species with trait values adapted to environmental conditions that are less common (Fig. 3a). An increase in functional divergence with spatial scale can be exacerbated if dominant species within a given environment at the site scale are located towards the centre of the functional space (Fig. 3a). Conversely, if the dominant species at the site scale are located towards the margins of the functional trait space (Fig. 3b), functional divergence should decrease with area. These patterns can occur simultaneously at landscape and regional scales, thus creating idiosyncratic functional divergence area relationships. For example, Karadimou et al. (2016), showed that because dominant plant species differed between volcanic islands, functional divergence did not change at the archipelago scale compared to the local, island scale. Changes in functional divergence could also appear without significant changes in species richness if there is an increase in the dominance of a reduced number of highly competitive and/or stress tolerant species with traits adapted to harsh, low resource conditions (Grime 2006, Mayfield and

Levine 2010). In this case, biotic sorting and environmental heterogeneity is expected to favour higher or similar levels of species richness, and an overall decline in functional divergence as disturbance level increases. Both our review (Fig. 4) and previous research has shown that scenarios where functional divergence increases with spatial extent are relatively uncommon compared to those where functional divergence decreases (Chalmandrier et al. 2017, Saar et al. 2017, Escobedo et al. 2020) or remains unchanged (Karadimou et al. 2016).

Expected relationships between functional evenness and species richness across spatial scales

Potential changes to functional evenness as spatial scale and disturbance intensity increase are numerous and more difficult to predict than changes in other functional diversity metrics. This is because high levels of functional evenness can reflect either that a low number of traits are evenly distributed across a reduced number of tolerant species (Fig. 3d–f), or that a high diversity of traits is evenly distributed across multiple species (Fig. 3g–i). The increase of functional evenness at landscape and regional scales will depend on how environmental variables acting at smaller spatial scales related to resource availability reduce, or increase, trait differentiation between dominant species (Shipley 2010, de Bello et al. 2013a). An increase in the proportion of environments that promote trait differentiation and an efficient use of multiple resources would drive high functional evenness (Fig. 3g–h). On the other hand, medium disturbance levels at landscape spatial scales are expected to increase functional evenness by favouring species with uncommon traits, if there is still enough habitat available to support them (Fig. 3h, Escobedo et al. 2020).

Empirical evidence about increases in functional evenness with species richness and spatial scale is rare. From our review, we found less than 20% of case studies where functional evenness was positively associated with species richness. This is because even if species are regularly distributed in the functional space, most communities are characterized by a few common species with a skewed tail of rare species, leading to an uneven repartition of abundances (Mouchet et al. 2010). A more feasible scenario consistent with empirical evidence (Biswas and Mallik 2011, Carmona et al. 2015, Karadimou et al. 2016), however, shows a negative relationship between functional evenness and species richness as spatial scale increases (Fig. 3e, h). As spatial scale increases, more rare species are recorded, increasing the total species richness and the functional trait space occupied (Carmona et al. 2016, Rossi et al. 2020). Simultaneously, more individuals of the common species are recorded thus the species abundance distribution at coarser scales is likely to become more skewed.

The influence of landscape structure and spatial autocorrelation

Biodiversity tends to be spatially structured across scales (Legendre 1993). At local scales, processes such as short-range seed dispersal, vegetative reproduction and intra and

interspecific competition act with environmental heterogeneity to shape the spatial distribution of species and traits (Zhang et al. 2015, Biswas et al. 2016, Martello et al. 2018). At landscape and regional scales, the spatial distribution of environmental variables such as soil, hydrology and climate are thought to drive the distribution of species with traits adapted to certain conditions. Therefore, while the area of natural land cover is a fundamental determinant of species richness and functional diversity (Fahrig and Triantis 2013), the shape and functional form of this relationship is expected to vary considerably depending on the spatial structuring of the environment (Box 1). Low spatially autocorrelated environments experience a full range of environmental variation over short intervals of space, and thus we expect high variation in functional richness as species richness increases with spatial extent. In contrast, in spatially autocorrelated environments, spatially adjacent locations tend to be similar and slow turnover in environmental conditions should result in relatively small increases of overall functional diversity as species richness increases with spatial extent. Despite support for their theoretical importance (Zhang et al. 2015, Biswas et al. 2016), generalities relating to how spatial autocorrelation impacts on the relationship between species richness and functional diversity across spatial scales remain elusive.

The importance of spatial structure driving functional diversity depends on how factors such as dispersal limitation and disturbance interact to drive species assemblage processes. An increase in disturbance in low spatially autocorrelated environments will favour an increase in generalist species with high dispersal and competitive abilities (Barbaro et al. 2014, Biswas et al. 2016). This increase in generalist species can decrease overall functional diversity by promoting trait convergence as spatial extent increases. High disturbance in low autocorrelated habitats can thus have negative effects on functional divergence and functional evenness over large (landscape, regional) spatial extents. On the other hand, spatially autocorrelated environments promote more stable conditions over more continuous areas and thus tend to increase the diversity of species (Rybacki et al. 2020). Since functional richness is correlated to species richness, landscapes with high spatial autocorrelation will tend to promote higher levels of functional diversity when compared to uncorrelated environments. Despite this, functional richness could increase faster than species richness in spatially uncorrelated versus correlated environments in small spatial extents if dispersal is limited among habitat patches (Box 1). Even though theory about the effects of spatial autocorrelation have been extensively discussed, most empirical work has focused on evaluating the spatial congruence between functional diversity and species richness (Devictor et al. 2010, Martín-Regalado et al. 2019). However, understanding the mechanisms that drive the spatial patterns of functional diversity is still a big challenge.

Several developments in spatial statistics make it possible to differentiate and quantify the mechanisms underlying spatial patterns of functional trait diversity across scales. Variation partitioning techniques (Peres-Neto et al. 2006)

Box 1

Environmental spatial autocorrelation affects patterns of functional diversity metrics across spatial extents. To illustrate this point, we simulated the spatial distribution for 50 communities from a regional species pool of 100 species using the individual based model described in Suárez-Castro et al. (2020). Community dynamics was simulated within landscape grids characterized by different levels of spatial autocorrelation in habitat values. Landscapes are grids of 50×50 cells where cell values represent a continuous measure of habitat type. Each cell has a fixed carrying capacity that can support a maximum of 10 individuals, which is constant across all cells in the landscape. Individuals' reproductive output in a cell depends on the distance between the habitat type value of each cell and trait values of that species. As this distance increases, the fitness of the individual decreases. In this simple scenario, functional diversity is defined using a single trait that determines the reproductive output of individuals in each cell. Trait values across species followed a distribution based on the parameters shown in Supporting information. Simulations were run for 100 generations, after which we

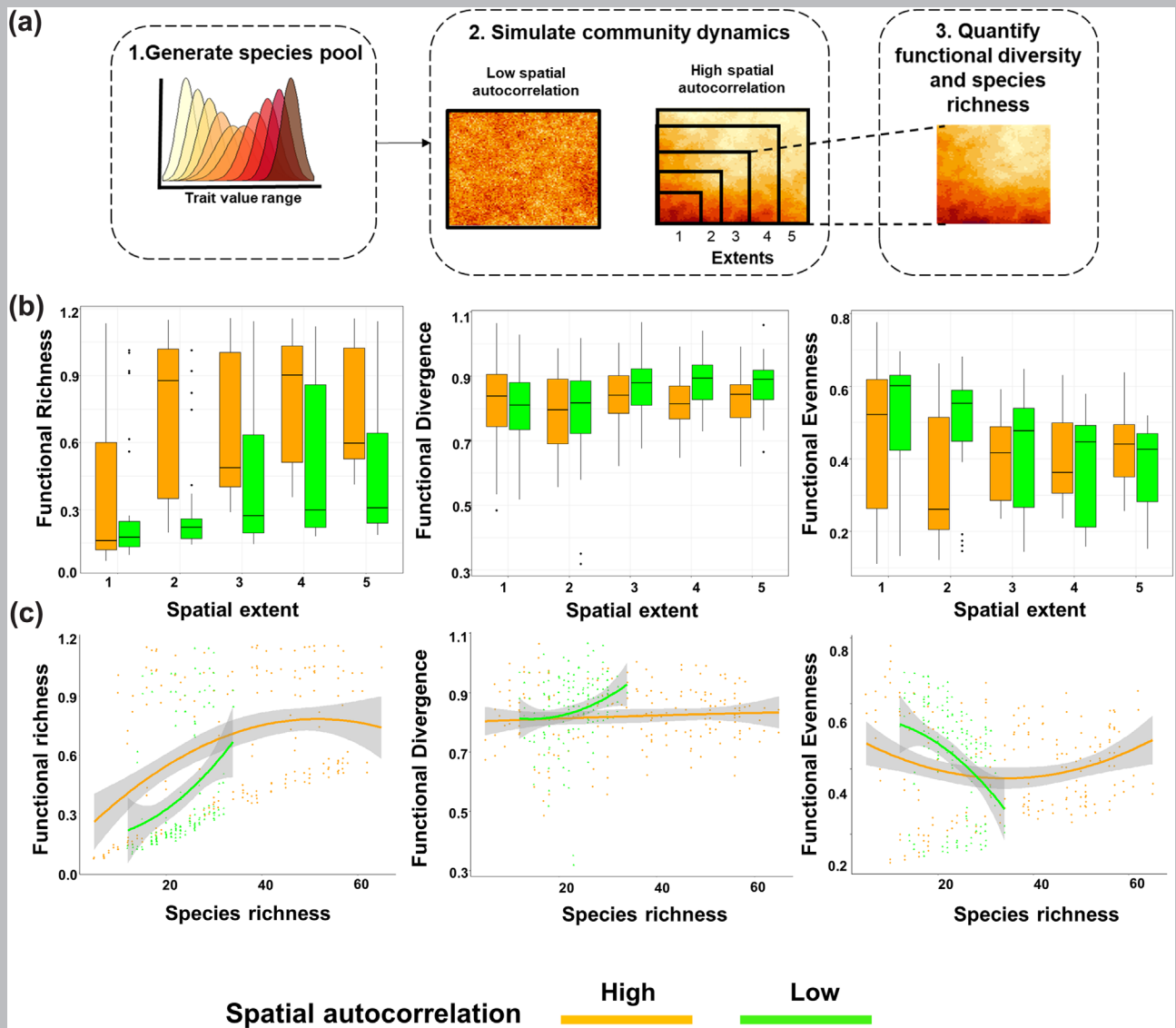


Figure Box 1. Effects of spatial autocorrelation on species richness and functional diversity across different spatial extents. (a) General approach used to calculate function diversity at different spatial scales for communities simulated in two contrasting landscape types with low and high spatial correlations. (b) Patterns of functional diversity metrics as a function of spatial extent in low and high spatially correlated environment. (c) Relationship between species richness and functional diversity in landscapes with different levels of spatial autocorrelation. Each point represents a different simulation. Grey areas represent the 95% confidence intervals of a nonlinear relationship. We only focused on one community type drawn from the same species pool. This approach could be expanded to test how different community types respond to spatially structured landscapes.

calculated three functional diversity metrics (functional richness, functional divergence and functional evenness) at five different spatial extents. More details of the modelling approach are described in Suárez-Castro et al. (2020). The code used to calculate the functional diversity metrics at multiple spatial extents, as well as the parameter values and initial conditions used for the simulations, are presented in the Supporting information. Environments with high spatial autocorrelation facilitate the coexistence of a high number of species as they tend to favour low dispersal, specialist species, as well as high dispersers that can colonize isolated areas. This is reflected in higher functional richness across scales (Fig. Box 1b), compared to landscapes where the low spatial autocorrelation tends to favour species with certain traits (e.g. high dispersers). High autocorrelated habitats also show more variation in functional richness at small spatial extents, because environments tend to be more contrasting when different areas of the landscape are compared. On the other hand, low spatially autocorrelated habitats can generate more heterogeneous environmental conditions at smaller extents. These conditions favour a steeper increase of functional richness as species richness increases over small areas (Fig. box 1c). Despite this, species richness is higher in high autocorrelated environments at large extents, even if values of functional richness remain similar compared to those at intermediate spatial extents. On the other hand, functional divergence and functional evenness can show similar values in both high and low autocorrelated environments. These metrics are not positively correlated with species richness (Fig. box 1c), and they can be invariant or even show a negative trend with increasing spatial extent (Fig. box 1b). In the case of functional evenness, a negative relationship with species richness can arise. This is particularly evident in low autocorrelated environments that tend to promote a high dominance of species sharing a reduced number of traits.

combined with spatial eigenvector mapping techniques (Kim 2013, Thayn and Simanis 2013), can be used to assess the relative contributions of environmental, biotic and dispersal limitation processes on variation in species and functional diversity (Biswas et al. 2016, Kim and Shin 2016). These methods allow for the decomposition of spatial autocorrelation into positive spatial autocorrelation and negative spatial autocorrelation (Biswas et al. 2016, 2017). Strong, positive autocorrelation means values tend to relate to global structure/large-scale patterns, as well as variation in local means. In contrast, negative spatial autocorrelation values reflect local fine-scale patterns and variation around local means. If simultaneous evidence of positive and negative spatial autocorrelation is found, this could be an indication that two processes are acting in opposition, one at a larger scale and one at a fine scale (Dray 2011). By contrasting positive and negative components of spatial autocorrelation for different indices of functional trait diversity, previous research has identified the spatial signature of multiple ecological processes acting at different spatial scales (Biswas and Mallik 2011, Zhang et al. 2015, 2018). For example, Biswas and Mallik (2011) and Biswas et al. (2016) found a strong spatial pattern of functional richness that matched with the spatial pattern of soil moisture, suggesting strong effects of environmental filtering on functional diversity. Interestingly, Biswas et al. (2016) showed that contrary to functional richness, functional evenness did not follow the spatial patterns of soil moisture, suggesting the increasing importance of local scale negative species interactions in structuring this community (Biswas and Mallik 2011).

Empirical evidence on how spatial factors and landscape context influence functional diversity and species richness across scales is accumulating. At local scales, extensive progress has been made in understanding how the frequency of disturbance alters functional diversity and species richness (Zhang et al. 2015, Kim and Shin 2016). At coarser scales,

there is copious evidence of how landscape composition affects species richness and functional diversity simultaneously (Mayfield et al. 2010, Luck et al. 2013, Newbold et al. 2013, Palma et al. 2015). However, there is still a lack of empirical evidence with which to evaluate how functional diversity changes across different levels of landscape structure (landscape composition and configuration). Theoretical evidence has shown that the relative importance of landscape fragmentation on functional diversity could be predicted depending on the variance in the distribution of species traits across species, as well as on the correlation among traits (Suárez-Castro et al. 2020). The higher the correlation and the variance among traits, negative effects of fragmentation on functional diversity tend to increase. However, most empirical studies are either conducted at the plot or fragment-level or do not distinguish between effects of landscape composition versus landscape configuration (Zambrano et al. 2019). As we are still unable to measure the net impact of landscape structure and spatial autocorrelation on functional diversity patterns across scales, we are limited in the extent to which we can apply trait-based frameworks to guide decision makers for managing changing landscapes.

The role of species interactions driving functional diversity and species richness across spatial scales

Overall ecosystem functioning is dependent on the variety and the type of species interactions represented in a community (Poisot et al. 2013, Schleuning et al. 2015, Gravel et al. 2016, Hallett et al. 2017). Since species traits mediate interactions between species (including competition, predation and mutualism), linking interaction network properties with trait-based approaches is important to understand the relationships between biodiversity and ecosystem

functioning (Lavorel et al. 2013). For example, interactions between fruit-eating birds and fruiting plants are, in part, determined by morphological traits such as beak shape on the one hand, and fruit length and diameter on the other (Dehling et al. 2014). The distributions of these resource and consumer traits thus jointly determine which seeds a bird is likely to disperse. Furthermore, the evaluation of species traits across trophic levels (e.g. differences in the body size of predators and prey), can give insights about the redundancy of traits of the interacting species (Gravel et al. 2013, Poisot et al. 2015, Laigle et al. 2018). However, despite their relevance, Gonzalez et al. (2020) showed that little theory and few empirical studies have directly addressed how interaction networks change with scale (but see Poisot et al. 2013, Barnes et al. 2016, Schieber et al. 2017, Galiana et al. 2018). Here, we show that our knowledge about the link between interaction network properties and functional diversity is also scarce. An important avenue of research thus consists on integrating information about the relationship between network properties, species richness and functional diversity.

Network structure changes with spatial scale

As spatial scale increases, species richness and/or patterns of species abundance change, modifying the distribution of species traits and thus affecting network structure. These changes in network structure depend on how new species either weaken existing interactions, for example through competition, or strengthen the links among trophic levels (Galiana et al. 2018). Take for example a hypothetical plant–frugivore network: if increasing the spatial scale of sampling causes the introduction into the network of a bird species with similar beak gape size to those species already present, its presence may weaken mutualistic interactions by competing for the same fruit resources. These species can be regarded as functionally redundant and therefore unlikely to add significantly to functional trait richness (Box 2). However, functional evenness and divergence may still be affected, as the number of interactions between species with specific trait associations become more important than others within the network (Laigle et al. 2018). Evidence from fragmented landscapes has shown that edge effects alter the abundance of generalist species without necessarily excluding specialists in plant–seed dispersers networks (Geslin et al. 2013, Novella-Fernandez et al. 2019). In this case, an increase in the dominance of generalist frugivores with a reduced set of traits decreases the evenness of interactions at landscape scales.

Network properties show different responses as spatial extent increases (Galiana et al. 2018). Properties such as link richness (Wood et al. 2015) and modularity (Montoya et al. 2015) have shown to linearly increase with species richness as spatial extent increases (Fig. 5a–b). For example, Wood et al. (2015) found that link richness of intertidal food webs increased by almost one order of magnitude when scales ranging from quadrat (0.25 m²) to archipelago (24 km²) were compared. Although these properties are correlated with species richness, their relationship with functional diversity is

still unclear. Higher modularity could indicate the existence of more functional groups (Maruyama et al. 2018), whereas an increase in link richness reflects a high number of specialized interactions between species with rare traits (Aizen et al. 2012). Thus, we would expect a positive relationship between modularity, functional richness and functional divergence (Box 2). However, evidence about the exact shape of this relationship is currently lacking. Furthermore, not all network properties increase with spatial scale. Bellmore et al. (2015), found that average interaction strengths in a food web were weakened when networks of individual aquatic habitat patches were aggregated at the floodplain mosaic scale. At this landscape scale, prey species (that were often strongly preyed upon at local scales) did not interact with predators as they found more opportunities for refugia (Fig. 5c). Notably, connectance, which describes the proportion of interactions realised between species (calculated as (link richness)/(species richness²); Williams et al. 2002) has shown to be either scale-invariant (Jordano et al. 2003, Maunsell et al. 2015, Morris et al. 2015) or decrease at regional spatial scales (Wood et al. 2015). This is because species richness tends to increase faster than the number of links as spatial extent increases (Galiana et al. 2018). In addition, several studies in plant pollinator networks have shown that nestedness is relatively independent of spatial sampling (Nielsen and Bascompte 2007, Rivera-Hutinel et al. 2012). This suggests that both at site and landscape scales, groups of generalist species tend to interact with small subsets of specialist species (Fig. 5d). Whether nestedness is influenced by specific traits and how this relates to spatial patterns across scales is still a main research gap.

Despite the clear understanding that traits are integral to network structures and that network properties respond differently to changes in spatial scale, current evidence is mixed and shows that changes in network structure can be reflected by certain aspects of the functional trait distribution, but not all (Saavedra et al. 2014, Gravel et al. 2016). A research gap thus consists on testing the covariation between functional diversity metrics and interaction network properties. For example, network properties may show different responses to changes in landscape extent even for the same increase in functional richness (Fig. 5). These changes depend on how dispersal among patches, competition and disturbance strengthen or weaken interactions between species. We thus need more evidence about the effects of multiple spatial attributes on network structure, key amongst which are edge effects (Novella-Fernandez et al. 2019), changes in landscape connectivity (Santos et al. 2019) and dispersal limitation. Linking spatial attributes to measures of functional diversity will allow us to infer, for example, how much species traits mediate the frequency by which consumers in a network feed on different resource species at patch and landscape scales (Dehling et al. 2014, Maruyama et al. 2018), as well as how dispersal rates shape the structure of a regional network compared to local scale networks (Galiana et al. 2018).

Another key aspect consists of identifying which traits are important in relation to network structure and which have

Box 2. Network properties and functional diversity

Different network properties can be used to assess the link between functional diversity, species richness and species interactions. Functional diversity and species richness may not necessarily increase at similar rates (i.e. a new species may fill a similar functional role as an existing species). If such redundancy exists, we also expect network stability to increase as the scale over which networks are examined changes. Here, we use four properties to illustrate this point: Modularity, Nestedness, Trophic complementarity and Link richness. Modularity (Fig. box 2a) describes how groups of species interact preferentially with members of their own group ('module'), more than others. In a plant–frugivore network, a module would be composed of bird and plant species with similar or overlapping traits, such that the birds are more likely to eat fruit from plants belonging to their own module. A higher modularity resulting from an increase in spatial scale thus indicates the existence of more functional groups (Maruyama et al. 2018). This metric is an indicator of niche partitioning, which can be reflected by an increase in both functional richness (more functional groups equals a wider range of traits) and functional divergence (clustering around the extreme ends of the trait value spectrum represented in each module) (Montoya et al. 2015). Nestedness (Fig. box 2b) is another property of network topology which describes a pattern whereby smaller groups of interacting species are a subset of larger groups (Bascompte et al. 2003). In trophic networks, nestedness arises out of differences in how consumers with certain traits (e.g. large body size) interact with a wider range of prey as the number of interacting species increase (Nordström et al. 2015). This property can thus be

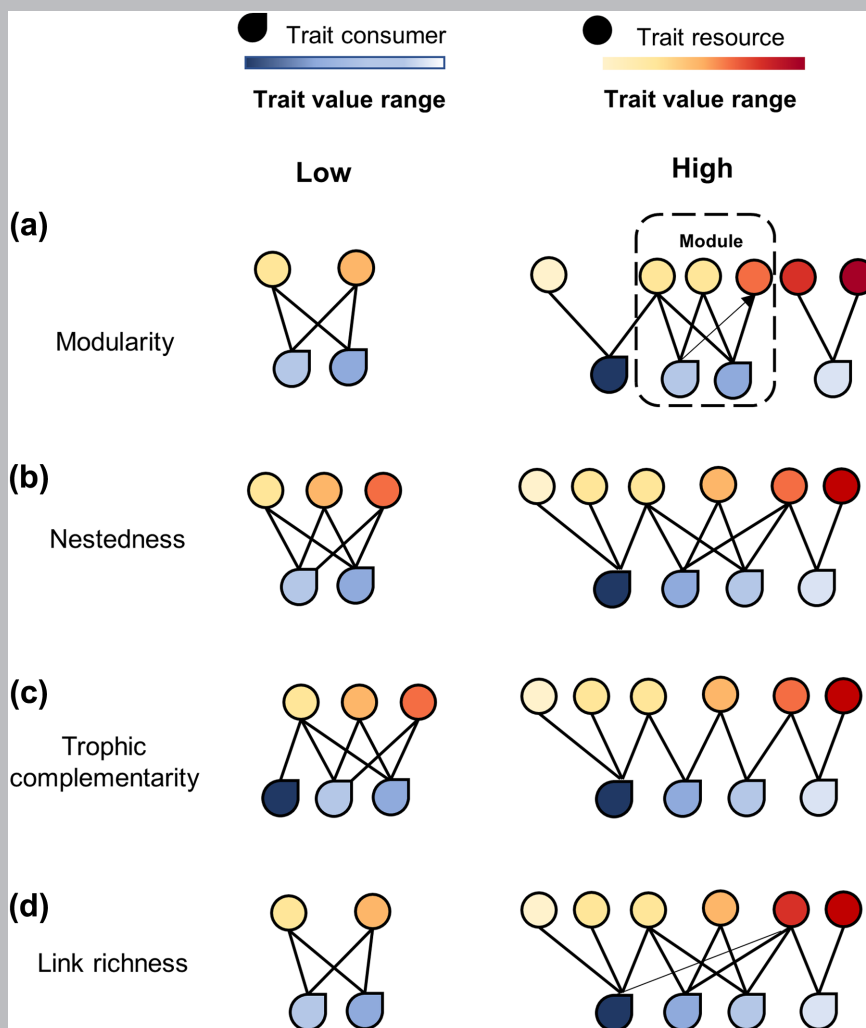


Figure Box 2. Schematic diagram of hypothetical positive relationships between network properties and functional trait diversity as species richness increases. Circles represent resource species and droplets represent consumers. Colours represent functional trait space.

related to functional richness of interacting species. Trophic complementarity (Fig. box 2c) uses the identity of a species' interaction partners to measure the uniqueness of its position within the food web, such that a resource species is defined by its consumers and vice versa (Poisot et al. 2013). Trophic complementarity is thus similar to modularity, but operates on a single trait axis (Montoya et al. 2015). An increase in trophic complementarity reflects the additive effect of new species to the network and thus a linear increase in species richness and functional richness. Link richness describes the number of interactions (links) in a network. High link richness (Fig. box 2d) suggests that more species interact with one another. If these new interactions involve rare, specialized species, an increase in functional richness is expected.

little to no effect. The effect of traits on ecological responses depends on the spatial scales of measurement (de Bello et al. 2013b, Suárez-Castro et al. 2018). Recent evidence has also shown that relationships between trait values and network properties can be better understood when looking at traits individually, than when considering functional diversity metrics (Laigle et al. 2018). Body size has a lot of potential in this sense because it can predict matching interactions between resources and consumers for a wide range of communities (Chamberlain et al. 2014, Poisot et al. 2015, Portalier et al. 2019). In addition, measuring body size might offer a

convenient way to gather a suite of covarying species traits into a single dimension, without necessarily having to observe all the traits directly (Woodward et al. 2005). Calculating functional metrics based on body size values could help to test how functional diversity reflects changes in network properties at multiple scales (Fig. 5). However, body size may not predict less common interactions that depend on other traits such as foraging strategies and predatory avoidance (Laigle et al. 2018). Moreover, other traits such as growth form and flower symmetry also play a predominant role determining the level of modularity in pollinator networks (Chamberlain et al. 2014).

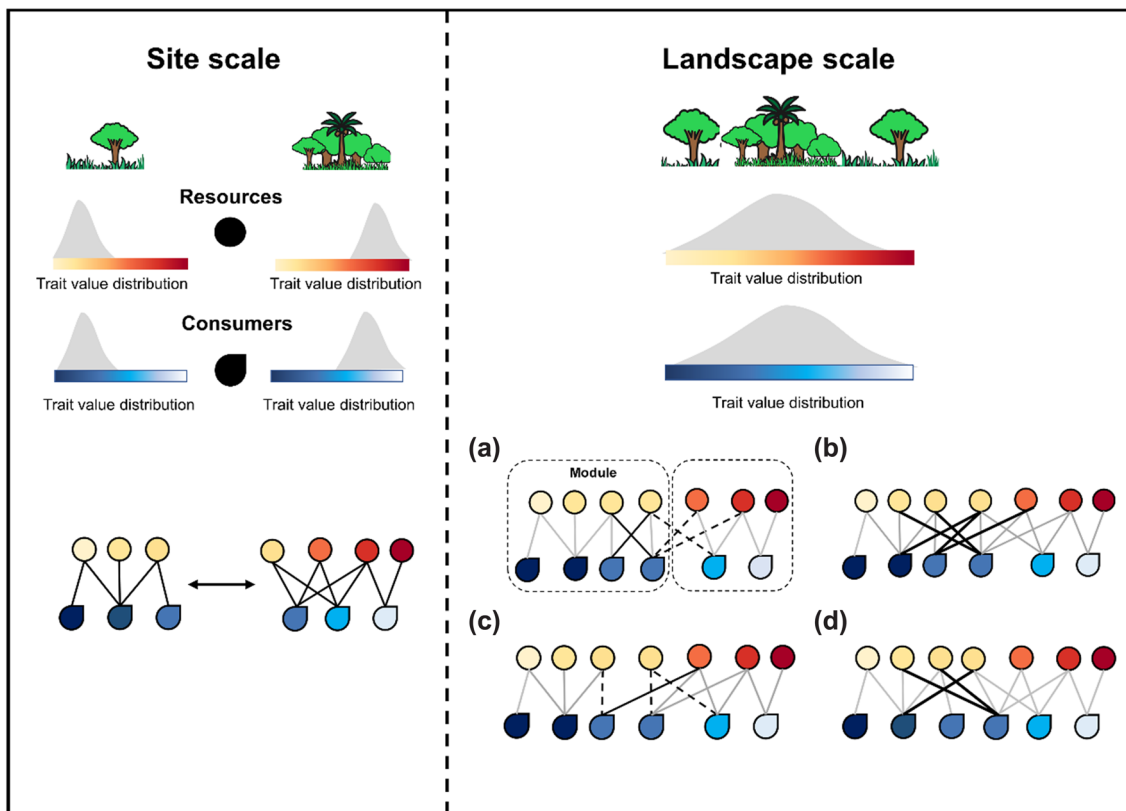


Figure 5. Similar increases in functional richness and species richness from site to landscape scales can have different effects on trophic network properties. These effects depend on the potential of individuals to disperse between habitat patches, environmental filtering, as well as the competitive ability of species that can strengthen or weaken links between species at landscape scales. In the right panel, grey lines represent existing interactions at the site scales that are unchanged at the landscape scale. Black lines represent new interactions and dotted lines represent weakened interactions. (a) Modularity and (b) link richness increase as the interactions between species sharing similar traits become stronger. (c) Some interactions are weakened either because species are displaced to consume other resources due to competition (black line), or because resources (prey) find more refugia at landscape scales. (d) Nestedness can stay the same (or even decrease) if more generalist species interact with species exhibiting a wide range of trait values at landscape scales.

Furthermore, several studies have shown that the importance of traits defining network interactions varies spatially. For example, Saavedra et al. (2014) found that body mass, gape width and wing tip length are important traits determining species interactions in the forest interior, but the interaction strength of bird species was not related to these traits at forest edges. The extent to which functional diversity explains the effects of landscape composition and configuration on species interactions is yet to be fully understood.

Towards an understanding of functional diversity and species richness relationships across spatial scales

Given the rapid conversion of natural habitats and the need for sustainable multifunctional landscapes in the long term (Haddad et al. 2015), evaluating how functional diversity changes across scales is a key research question. Our synthesis shows that progress has been made studying the relative effect of environmental filtering and selection processes on species richness and functional diversity simultaneously (Biswas and Mallik 2011, de Bello et al. 2013a, Escobedo et al. 2020). However, a multiscale framework integrating the effects of spatial autocorrelation on functional diversity and the variation in the structure of species network interactions is missing. Figure 6 summarizes some of the key opportunities of research that we have identified to understand the relationship between species richness and functional diversity across multiple spatial scales.

Testing patterns described in this synthesis with data collected across multiple regions will help to advance this area of research. To do so, empirical studies can benefit from the current development of large databases (Kattge et al. 2011, Salguero-Gómez et al. 2015) and remote sensing methods (Jetz et al. 2016, Spasojevic et al. 2016, Schneider et al. 2017, Rossi et al. 2020). Remote sensing data can improve the simultaneous extraction of multiple trait values across large extents, a task that is extremely time-consuming in field campaigns. Active remote sensing technologies such as Sentinel-2 satellites, synthetic active radar (SAR) and light detection and ranging (LiDAR) instruments help to monitor plant traits at very high resolutions (e.g. 10 m) and spatial extents (Durán et al. 2019, Ma et al. 2020). For example, Durán et al. (2019) used both imaging spectroscopy and foliar traits to estimate functional diversity in tropical forests across a large elevation gradient (215–3537 m) in South America. These authors were able to find scale-dependent signals of trait convergence that were associated with environmental filtering. A key issue, however, consists of addressing spatial scale mismatches between data collected from field surveys and remote sensing methods (Ma et al. 2020). When using data from field surveys, trait values are typically averaged to the species level and then aggregated to community estimates of functional diversity accounting for species abundance. On the other hand, remote sensing methods estimate functional diversity

as the variance of trait values among pixels. New technologies such as hyperspectral sensors onboard small unmanned aerial vehicles have a great potential to integrate data obtained from different methodologies (Capolupo et al. 2015).

As more data becomes available, researchers will be able to identify the implications of using metrics that combine multiple traits to understand functional diversity patterns across regions. In this synthesis, we mostly focused on single trait examples to illustrate expected changes in functional diversity with spatial scale. However, the success of an organism in a particular environment depends on more than one trait (Kraft et al. 2015, Cadotte 2017). In addition, the relationship between functional diversity, species richness and network structure is likely to depend significantly on the identity of the chosen traits (Weiss and Ray 2019). Although multivariate metrics of functional diversity are important in explaining niche differences across species, approaches combining multiple traits into one metric could obscure inferences about trait differentiation along axes that allow coexistence of species or persistence in a habitat (Butterfield and Suding 2013, Chalmandrier et al. 2017). Therefore, reporting both univariate and multivariate functional diversity–area relationships should become a standard practice for future studies using multiple traits to determine how trait dispersion patterns depart from null expectations along the scale gradient (Smith et al. 2013, Múrria et al. 2020).

More work is needed to understand how landscape structure affects functional diversity metrics. A key question consists of identifying how edge effects and connectivity promote or impede interactions among individuals and thus influence the spatial structure of functional diversity (Barbaro et al. 2014, Craven et al. 2016, Ruffell et al. 2016). For example, previous work has found that bird insectivory increases at edges and in small forest fragments (González-Gómez et al. 2006), and this increase may be explained by higher levels of functional evenness and functional divergence in edge compared to interior bird assemblages. Functional diversity patterns also change depending on how connected habitat patches across the landscape are. Liu and Wang (2018) showed that functional richness in unconnected lakes from the Yangtze River basin was lower compared to functional richness in connected lakes. Despite this, most studies evaluating functional diversity across scales focus on comparing areas with different proportions of land covers and levels of disturbance, but the effects of landscape structure context and their relationship with changes in species interactions are largely ignored. Although spatially explicit analyses that quantify the relationship between functional diversity and species richness have become more common, this area of research is still relatively unexplored. Methods such as distance-based Moran's eigenvector maps and variance partitioning analysis (Zhang et al. 2015, Biswas et al. 2016) can help to understand how the spatial distribution of functional diversity reflects the interacting effects of environmental filtering, dispersal limitation and competition across spatial scales.

Another aspect that should be considered is identifying how network properties are related to functional diversity at

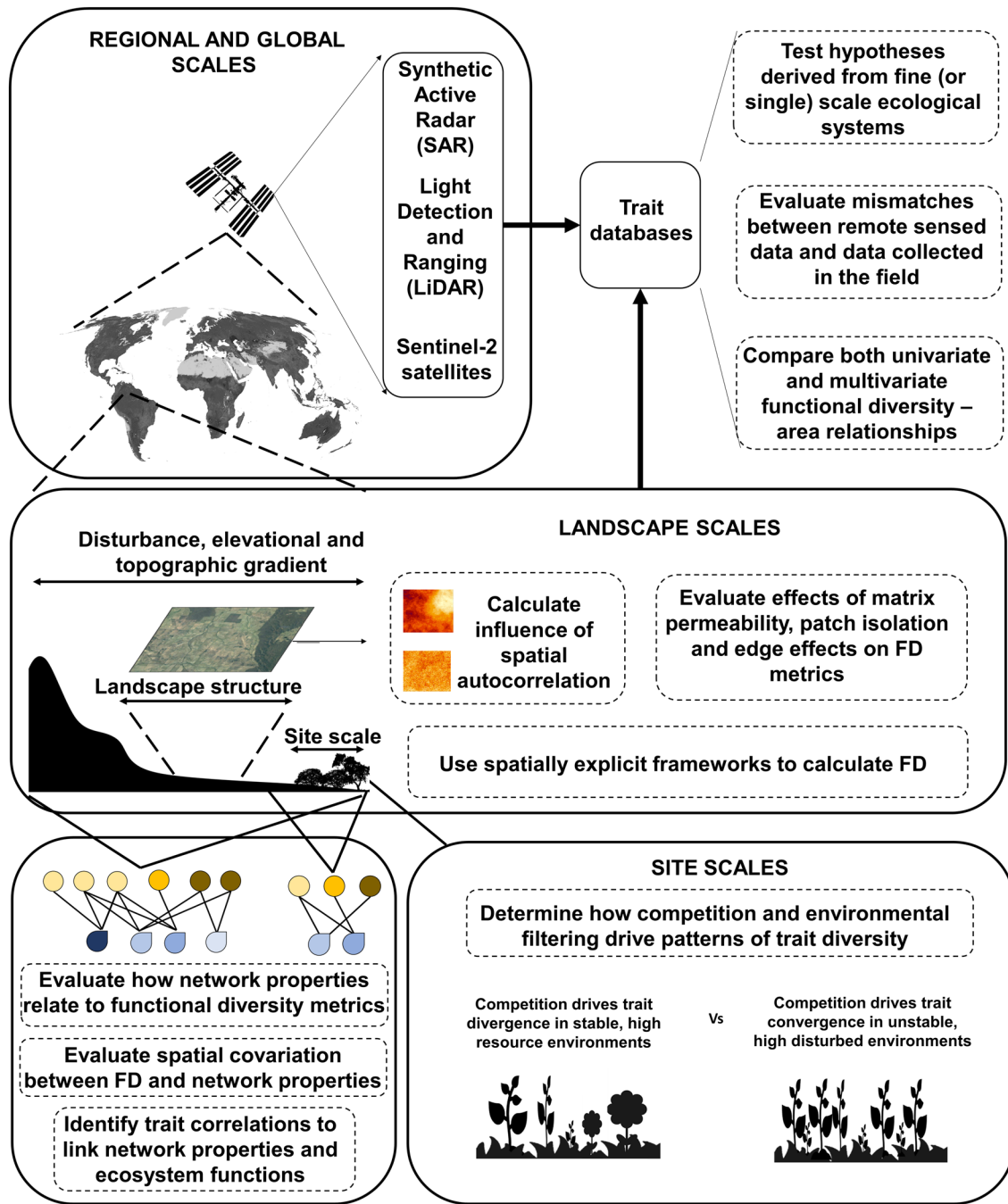


Figure 6. Key opportunities of research to understand the relationship between species richness and functional diversity across multiple spatial scales.

different spatial scales, and how this is related to ecosystem functioning. As explained by Gravel et al. (2016), linking the spatial variation between functional diversity, network properties and functioning is not a common practice in ecology. A way towards solving this research gap could consist of identifying how traits of interacting species are correlated, and how do they vary spatially across scales. The first step to achieve this could be identifying those traits that are most important in determining the effect of species on ecosystem functions (effect traits; Mori et al. 2013, Bu et al. 2019), and traits

that determine species vulnerability to environmental change (response traits; Suding et al. 2008). Theoretically, a loss of effect traits should translate to losses in ecosystem functions, and this should be reflected in the loss of interactions among trophic levels (e.g. loss of large seed dispersers). By measuring the correlation between response and effect traits, we could potentially measure how effects of environmental change on community structure (measured by response trait diversity) translates in a predictable way to changes in network structure and ecosystem functioning (Lavorel et al. 2013).

Representing the spatial variation of the correlation among traits within a network is thus of great interest as it could reveal effects of environmental filtering across environmental gradients and spatial scales (Gravel et al. 2016).

Our synthesis presents an overview of some key elements needed to evaluate the relationship between species richness and functional diversity within a spatially explicit, multi-scale framework. Theoretical and empirical evidence at fine scales have provided important insights of how competition and environmental filtering drive patterns of trait diversity (Mayfield and Levine 2010, Shipley 2010, Saar et al. 2017, Escobedo et al. 2020). Upscaling these insights across multiple spatial scales requires a consistent methodology to evaluate how spatial variables and disturbance promote the coexistence of individuals with different traits, independently of their species identity. As more data is collected, spatially explicit methods can benefit from metrics that measure functional diversity within trait probability density frameworks. Trait probability density frameworks allow to standardize measures of different components of functional diversity independently of the scale considered (Carmona et al. 2016), and thus could help to compare relative patterns of functional diversity between different regions. However, these sophisticated approaches are still difficult to apply due to a general lack of data of trait intraspecific variability. In addition, even if this data is available, most of our understanding of the relationship between species richness and functional diversity still comes from non-spatially explicit, single scale analysis. A better integration and communication between the fields of landscape and community ecology is needed if we want to advance in this important area of research.

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Author contributions

Andrés F. Suárez-Castro: Conceptualization (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Project administration (lead); Writing – original draft (equal); Writing – review and editing (equal). **Maia Raymundo:** Conceptualization (supporting); Formal analysis (supporting); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Malyon Bimler:** Conceptualization (supporting); Formal analysis (supporting); Investigation (equal); Writing – original draft (equal); Writing – review and editing (equal). **Margaret Mayfield:** Conceptualization (equal); Methodology (equal); Writing – review and editing (equal).

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Data availability statement

This paper contains no original data.

Supporting information

The supporting information associated with this article is available from the online version.

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