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The drivers of species turnover

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CONTENTS

ABSTRACT

A key challenge in ecology is to understand why there are different species in different places on our planet. Species diversity in a community is the result of a multitude of processes and events in space and time. Species turnover is the variation in species identities among sites, but the factors causing turnover are debated. The aim of this essay is to review the literature and examine some of the mechanisms that are hypothesized to drive species turnover among sites. Species turnover can be determined by the regional species pool, climate, landscape structure, disturbance, species interactions, and dispersal. Important are also interactions among these factors. The life history characteristics and the distribution of resources in the landscape can also determine species turnover. In several studies, the importance of the scale of observation on species turnover is highlighted. This is due to that factors can be more or less relevant depending on scale. For instance, biotic interactions are more important at a local scale while environmental heterogeneity usually becomes more relevant at a larger scale. Understanding the main drivers of turnover is difficult due to the numerous factors that influence community composition and the complex interactions between them. However, the development of concepts such as the regional species pool, niche, connectivity, metapopulations and so forth, have aided in disentangling each mechanism and their relevance at different spatial scales. Turnover metrics are useful tools to understand the effects of ecosystem change on biodiversity and they should be used in combination with theory in order to better understand the effects of ecosystem change on biodiversity.

INTRODUCTION

A key challenge in ecology is to understand why there are different types and numbers of species in different places around the planet (Palmer 1994, Rosenzweig 1995, Leibold et al. 2004, Vellend 2016). Biogeographical diversity patterns can often be explained using a focus on evolution and historical occurrences, whilst species richness patterns can be related to ecological processes. This is because patterns of distribution, abundance and interaction vary with the scale of observation (Levin 1992, Whittaker et al. 2001, Leibold et al. 2004). In other words, the mechanisms and dynamics that are important in an ecosystem at the local scale may not be important at the regional or at the global scale. Because of this, Whittaker (1972) proposed three definitions of diversity based on the spatial scale: (1) the local community's richness in species (α diversity), (2) the extent of differentiation of communities along habitat gradients (β diversity), and (3) the overall diversity of the landscape, based on the α and β diversity of the communities in that landscape (ϒ diversity).

Ecologists have defined three components of diversity: local species richness, spatial turnover or differentiation diversity and regional species richness (Whittaker et al. 2001). Spatial turnover and β diversity are often interchangeably used and defined as the variation in the species identities among sites. There are two main ways to define β diversity: as species turnover along a gradient or as among-plot variability in species composition. β diversity as turnover measures the change in community structure between samples along a gradient. Turnover can be expressed as a rate and presented as a distance-decay plot: the 'distance decay of similarity'. The second type of β diversity index measures the variation in community structure among a set of sample units (Vellend 2001, Anderson et al. 2011). The relationship between species richness and species turnover varies with spatial scale. Turnover is high when the proportion of species shared between two areas is low, and when the proportions of species lost and gained moving from one area to the other are similar (Koleff and Gaston 2002).

β diversity can be partitioned into two main components: turnover and nestedness (Baselga (2010) . Turnover, as seen above, refers to species replacement while nestedness occurs when species assemblages in species-poor sites are a subset of the assemblages in more species-rich sites. There have been many hypotheses as to why there is species turnover. These include environmental heterogeneity and filtering, biotic interactions, landscape structure, dispersal, disturbance regimes, species-area, and species-time relationships (Ricklefs 1987, Nekola and

White 1999, Soininen et al. 2007, Kraft et al. 2011, Brown 2014). All of these are dependent on the scale of observation and the taxon, meaning that there is no one scale at which to describe populations or ecosystems (Levin 1992, Rosenzweig 1995, Whittaker et al. 2001, Chase and Leibold 2002). There can also be interactions among local and regional factors (Brown 2014). Ecological systems are therefore subject to different interacting biotic and abiotic factors that work on different spatial and temporal scales and which are also subject to stochasticity. Understanding species distributions is a challenging task, and the aim of this essay is to review the mechanisms that drive species spatial turnover.

FILTERING AND THE REGIONAL SPECIES POOL

There is a growing recognition that many of the processes that drive variation in species diversity occur at scales larger than scales at the community or landscape level. Biogeographical and evolutionary processes e.g. speciation, migration and extinction, directly influence communities, but influence also diversity at large spatial and temporal scales (Kraft et al. 2011, Cornell and Harrison 2014). However, distinguishing between local and regional factors is a difficult task because of the interactions that occur between them (Partel et al. 2016). In the effort of separating these factors, several theories have been developed that take into account a regional species pool. In general, a regional species pool is the set of species that are available to colonize a locality regardless of their ability to tolerate the environmental conditions (Srivastava 1999, Cornell and Harrison 2014). The theory of Island biogeography proposed that species diversity on individual islands depends on immigration from a mainland species pool (MacArthur and Wilson 1967). In addition, neutral theory (Hubbell 2001) has also depicted local communities as samples from a regional pool (Cornell and Harrison 2014). Thus, the regional species pool is important for community structure, which in turn is governed by a continuum of processes that include dispersal, environmental filtering, and niche occupancy. These processes have been conceptualized as a number of filters that determine community diversity (Figure 1; Leibold et al. 2004, Cornell and Harrison 2014, Kraft et al. 2015, Vellend 2016).

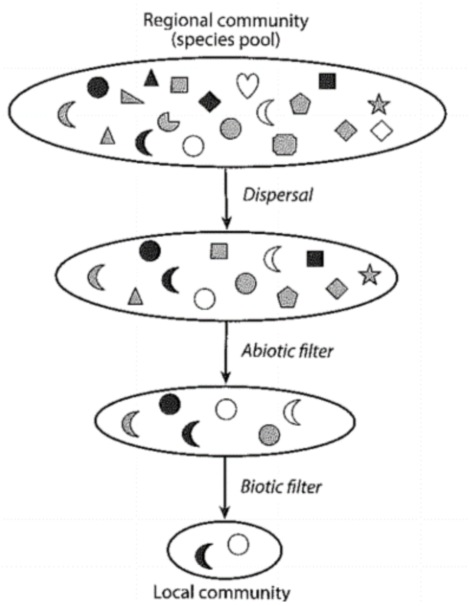

Figure 1. The filter model of community assembly depicts the relationship between regional diversity and community diversity through a set of filters. First, the regional species pool is governed by biogeographical and evolutionary processes. Then, the regional species pool is subject to dispersal barriers which can explain why a certain species is absent from a community. Next, environmental filtering occurs when a species that was successful at arriving to a locality was unable to tolerate the abiotic conditions and could therefore not establish. Finally, competition, disturbances and natural enemies eliminate the species that could establish and tolerate the environment. Thus, the species that are present in the community have passed through several biotic and abiotic filters and can therefore coexist (Source: Vellend 2016).

The characteristics of the regional species pool can affect the turnover of local communities. For instance, the size of the regional species pool is an important factor. If the regional species pool is small, it will be similar to the number of species that can coexist locally and therefore local communities will be relatively similar in structure, thus reducing species turnover (MacArthur and Wilson 1967, Chase and Leibold 2003, Stegen et al. 2013). In addition, the species pool could have its greatest influence over local communities mostly when they are not governed by species interactions (e.g. when the communities are under frequent disturbance; Cornell and Harrison (2014)) .

It is often difficult to separate the outcomes of environmental filtering of species from those of biotic interactions. It is in general true that not all organisms will be able to establish and persist in all places due to the abiotic conditions, but the absence of a species in a community can be the result of either environmental filtering or of competition, given that the species is present in the regional species pool. Ultimately distinguishing between the outcome of biotic interactions and environmental filtering could be related to scale: at a big enough scale, the species turnover will be more than evident when comparing habitats (e.g. a desert vs. a wetland). At a smaller scale, biotic interactions will become more important for determining the composition of communities. Therefore it is important to determine at which spatial scale that environmental filtering becomes more relevant than biotic interactions (Cadotte and Tucker 2017).

ABIOTIC FILTERS

Species have an optimum response to a set of environmental conditions. These conditions are referred to as the fundamental niche of a species, (Hutchinson 1957, Anderson et al. 2002). As conditions deviate from the optimum, the species will be less likely to occur (Palmer 2007). In consequence, the environmental heterogeneity hypothesis states that the more heterogeneous (spatially variable) a region is, the more species it will contain (Palmer 2007). Because of this, the idea that the abiotic environment shapes the distribution of species across the landscape has been one of the most enduring concepts in ecology (Kraft et al. 2015). This line of logic leads to the conclusion that localities with similar abiotic conditions have communities with similar composition and similar functions. In addition, an environmental gradient would allow for differentiation between functional identities of species along the gradient (Ricklefs 1987, Chase and Leibold 2003). However, ecologists have not succeeded in demonstrating the uniformity of the environmental filter concept. A possible reason is that the abiotic environment can affect community assembly and maintenance both directly and indirectly (Ricklefs 1987, Kraft et al. 2015). Temperature, sunlight, water and nutrients directly affect community assembly and structure by preventing the establishment or persistence of a species in a particular location (Brown 2014). Abiotic conditions can indirectly influence the outcome of biotic interactions ultimately affecting community composition. If the species within a community differ in their responses to abiotic conditions, then a heterogeneous local environment can indirectly influence the structure of the community because the outcome of the biotic interactions will depend on the environment (Kraft et al. 2015). Thus, environmental variables are often insufficient to predict the distribution of species (Ricklefs 1987, Brown 2014).

Environmental heterogeneity effects can also be confounded with the effects of resource availability (Yang et al. 2015). Primary production is a factor influencing community assembly at a local scale. For instance, Chase and Leibold (2003) argued that only species with high tolerance can survive in low productivity regions, and that the number of species in the locality will also increase with increasing productivity. Accordingly, there would be high species turnover between sites with low and high resource availability. Supporting this hypothesis is the fact that deserts hold a low amount of species because the abiotic conditions is such environments are too constraining for organisms to convert energy and nutrients into biomass (Brown 2014). Area and spatial environmental heterogeneity can also have a conflicting effect on species turnover because of area-heterogeneity trade-offs. As environmental heterogeneity increases, there will be a reduction in area of suitable habitat for particular species. This would consequently reduce species richness through different mechanisms like an increase in the likelihood of stochastic extinctions, a reduction in the amount of available resources, or inbreeding. Thus, the area-heterogeneity trade-offs ultimately promotes species turnover (Connor and McCoy 1979, Drakare et al. 2006, Allouche et al. 2012, Stegen et al. 2013).

Despite of this, environmental heterogeneity is regarded to be one of the most important factors governing community structure. Spatial environmental heterogeneity promotes species diversity through three mechanisms: 1) increased coexistence among species due to increased niche space, 2) promoting species persistence due to a higher number of shelter and refuges from harsh environmental conditions, and 3) promoting speciation and adaptation of species (Stein et al. 2014). Thus, environmental heterogeneity ultimately promotes large-scale spatial turnover by favoring species that thrive in different habitats (Stein et al. 2014, Stein and Kreft 2015). Accordingly, Stein et al. (2014) found that the influence of environmental heterogeneity on species turnover will always be dependent on the scale of observation.

BIOTIC FILTERS

A species fundamental niche is usually restricted by the presence of competitors or predators. This reduces the niche that can actually be exploited it into a fraction of the fundamental niche. This realized niche is dictated by intra- and interspecific competition and predation (Hutchinson 1957, Anderson et al. 2002). Biotic processes such as predation, disease or competition are usually local in nature and affect whether or not the species is present or absent in an area (Ricklefs 1987). There have been a number of hypotheses on the effects of competition on local diversity (e.g: Gause 1934, Paine 1966, Sanders 1968, Levins and Culver 1971, Tilman 1982, Holt et al. 1994). For instance, the competitive exclusion principle states that two species competing for the same resource cannot coexist because one or the other will inevitably have at least a small advantage and will eventually cause the disappearance of the other species (Gause 1934, Tilman 1982). The competition-relatedness hypothesis proposes that closely related taxa compete more intensely than distantly related counterparts (Cahill et al. 2008, Mayfield and Levine 2010). Consequently, competitive exclusion is expected to have a negative effect on spatial turnover because it would ultimately lead to the same competitively superior species being present in all local communities (Segre et al. 2014). However, while studying Mediterranean grasslands Segre et al. (2014) found that the effect of interspecific competition on spatial turnover can be either negative or positive, and that the outcome depends on environmental factors and the scale at which the patterns are examined.

Predation can also affect the outcome of interspecific competition. Paine proposed that predation on dominant competitors can prevent them from monopolizing a major food resource and that predation can also act to reduce the intensity of competitive interactions between species in lower trophic levels (Paine 1966, Paine 1971). In other words, predators (e.g. any organism that has a negative effect on the population growth rate of a species by consuming part or all of prey individuals) keep species in lower trophic levels below their carrying capacities. This allows new species to enter the community, changing species composition and positively affecting species turnover (Menge and Sutherland 1976, Chase et al. 2002). As a result, predation can have different effects on the geographical distribution of species. This effect can be direct; by consuming the individuals of another species, which could result in an absolute reduction in population density of the prey, on indirect; by reducing competition between individuals in the same trophic level allowing colonization by new species (Chase et al. 2002). The distribution of the predator can in turn be affected by the distribution of their prey if the predator is very specialized and feed only on a small number of prey. For example, the brimstone butterfly *Gonepteryx rhamni* has been shown to extend its geographic range after the host plants were planted outside their natural ranges in the U.K. (Gutiérrez and Thomas 2000). Pathogens can also affect species geographical distributions by eliminating species locally or entirely, positively affecting species turnover (Chase et al. 2002).

The relative impact of local vs. biogeographical processes on community structure depends in part on the strength of the biotic interactions within a local habitat. The structure of communities with strong biotic interactions among species at the same trophic level will mostly depend on local processes such as predation, parasitism, competition, and disturbances. On the other hand, the structure of communities with weak local species interactions will depend more on the size and composition of the regional species pool and processes in broader scales such as dispersal, speciation, widespread extinction and fluctuation in species distributions (Cornell and Lawton 1992).

DISPERSAL AND COLONIZATION-EXTINCTION DYNAMICS

Dispersal occurs for many reasons: e.g. to search for resources, to avoid harsh conditions, predators and competition, to be near conspecifics, and to maximize the number of descendants in space. Furthermore, dispersal and how far an organism can disperse can be influenced by a number of factors related to the species and/or individual and the environment. For instance, variation in body size or the stage in the life cycle can affect how far a species can disperse. Additionally, the structure and connectivity of the landscape and home range size can set a limit to dispersal distance (Southwood 1977, Rosenzweig 1995, Bowman et al. 2002, Jenkins et al. 2007, Bolnick et al. 2011, Kraft et al. 2011, Vellend 2016, Gallagher et al. 2017). One factor that could be influencing dispersal are density-dependent processes (Baguette and Schtickzelle 2006). Density-dependent processes are influenced by demographic parameters such as birth, death, immigration or emigration in the population (Price et al. 2011). Rates of immigration and extinction can determine species turnover. If the rates of immigration or extinction are high, there can be complete species turnover. If immigrations exceed extinctions or *vice versa*, turnover rates may also be high (Hillebrand et al. 2018). The density of conspecifics has been suggested to influence dispersal activity both negatively and positively. In butterflies, both circumstances have been found; in some cases, individuals disperse at higher rate away from low density local populations (low density-dependent dispersal) and in others butterflies disperse at higher rates away from high conspecific density (Enfjäll and Leimar 2005). Dispersal can affect β diversity depending on the size of the population: in small populations, emigration can increase the risk of local extinction (positively affecting species turnover), while immigration can reduce it (Hanski 2001).

Source-sink dynamics, (i.e. effects of habitat specific demographic rates on population growth and regulation, Pulliam 1988), are more likely to become apparent when habitat patches differ in quality because they can lead to an increase in differences of local population abundances. Sources are areas in which species have positive population growth and sinks are areas where they would show negative population growth without immigration. These dynamics lead to mass effects, which refer to the establishment of species in sites where they otherwise would not be able to self-maintain (Shmida and Wilson 1985). Populations that receive a flow of individuals from source populations have subsequently a reduced risk of extinction due to immigration (i.e. rescue effects) (Brown and Kodric-Brown 1977, Hanski 2001). Dispersal and mass effects allow rescue effects and create induced density-dependent stability in predator-prey interactions (Hoopes et al. 2005). In other words, dispersal may facilitate the persistence of prey species and inferior competitors in communities that reside in habitats with different degree of quality, which affects species turnover negatively. On the other hand, mass effects and high dispersal rates can also lead to a reduced local and regional diversity because they can facilitate the regional establishment of dominant competitors or generalist predators and ultimately reduce species turnover (Vanschoenwinkel et al. 2013).

The rate of dispersal within the regional species pool can, depending on the attributes of the landscape, increase the similarity among local communities and thus reduce species turnover. On the other hand, a low dispersal ability will lead to the aggregation of species at different localities and there will therefore be high turnover of species due to a higher α diversity (MacArthur and Wilson 1967, Chase and Leibold 2003). Thus, dispersal is known to be a determining factor influencing species distributions but it is difficult to isolate and quantify its effects on local diversity (Wandrag et al. 2017). However, the isle of Guam in the Western Pacific presents a unique situation: the complete loss of vertebrate seed dispersers. By making use of this situation, Wandrag et al. (2017) managed to quantify the contribution of seed dispersal by vertebrates to the spatial patterns of tree seedling diversity. They found that the complete loss of vertebrate seed dispersers in Guam has led to a decreased dispersal of seeds and ultimately to a doubling of species turnover on the island. In contrast, two other islands, Rota and Saipan, had vertebrate dispersers present and tree species turnover was significantly lower compared with that of the island of Guam.

LANDSCAPE STRUCTURE

Habitat loss and degradation have forced many animal and plant populations into remnant habitat patches spread throughout the landscape and populations that inhabit isolated habitat patches are at risk of local extinctions. However, a network of habitat patches may allow species survival if the patches are interconnected by dispersal (Moilanen and Hanski 1998, Holyoak et al. 2005). At the metapopulation level, dispersal and colonization of new habitat patches is a very important mechanism for the long-term persistence of species, and it compensates for local extinctions, reducing species turnover. Thus, dispersal can be viewed as a form of risk-spreading, enhancing population growth rate and the persistence of metapopulations that consist of populations with independent dynamics (Hanski and Gilpin 1991, Hanski 2001).

Local extinctions must be balanced with (re)colonization of habitat patches in order for regional populations to survive. Changes in land use that lead to the breaking apart and loss of habitat can ultimately lead to isolated habitat patches. These changes in landscape structure can affect the ability of organisms to disperse between patches (Jonsen and Fahrig 1997). However, the differentiation between matrix and the habitat patch is species-specific. This is because what is considered the matrix for one species can contain resources for another species and thus classify as habitat (Dover and Settele 2008). As a result, the spatial dynamics of the species will depend on their perception of their surroundings, which is in turn influenced by their level of habitat specialization. The degree of a species’ habitat specialization will influence how the organism perceives the size of their habitat and how isolated their patches are (Harrison 1997). For instance, generalist insects are able to persist when they can supplement their resources with those found in other habitat types. This is known as habitat supplementation, and is the ability of an organism to utilize more than one habitat within the landscape (Jonsen and Fahrig 1997, Tscharntke et al. 2012). Therefore, generalist species have a larger spatial extent than habitat specialists and habitat specialists can thus experience habitat patches as more isolated, which hinders their dispersal ability (Jonsen and Fahrig 1997). This can lead to high species turnover between habitat patches because specialist species will be confined to patches that can sustain local populations whilst they go locally extinct from small and/or low quality patches.

Connectivity, a key concept in spatial ecology, incorporates all aspects affecting the movement of an individual among resource or habitat patches within landscapes and is defined as “the degree to which the landscape facilitates or impedes movements among resource patches” (Taylor et al. 1993, Baguette and Van Dyck 2007, Baguette et al. 2013, Auffret et al. 2017). Connectivity can be viewed from two different perspectives: functional connectivity and structural connectivity. Functional connectivity depicts how the structure and elements of the landscape affect the behaviour of a dispersing organism. Structural connectivity refers to the configuration of habitat patches in the landscape and the presence of dispersal barriers (Baguette and Van Dyck 2007, Auffret et al. 2017). If the landscapes are structurally different, species turnover between local communities will be high (Laurance et al. 2007, Tscharntke et al. 2012). For example, bee and wasp β diversity was higher in the complex landscapes when comparing between structurally simplified landscapes (e.g. agricultural landscapes) and more complex, heterogeneous landscapes (Tylianakis et al. 2005). In addition, mortality risks during dispersal increase with the distance between patches in the landscape, which could positively affect species turnover (Baguette and Van Dyck 2007).

The behaviour and space use of individuals can be affected by the distance and area at which they gather information. The smallest scale at which an organism perceives spatial heterogeneity is referred to as the grain size of the landscape. (Baguette and Van Dyck 2007). A given landscape can represent high connectivity for some species but low connectivity for other species because of the grain of the resource configuration in the landscape. For arthropods, the physical characteristics of habitat boundaries, such as height or foliar density, may affect their willingness to leave a patch. The movements of butterflies can be influenced by both local and landscape features. This is because the responses to landscape features can be explained by edge-related resource distributions. In addition, butterfly species that are related may respond similarly to the same features (Kuefler and Haddad 2006). Even when the borders of habitat patches are diffuse, colonization-extinction dynamics or mass effects could influence community structure in different spatial and temporal scales (Leibold et al. (2004). On the other hand, it has also been argued that it is difficult to account for colonization-extinction dynamics in species turnover between sites when there is species spillover from the matrix (Tscharntke et al. 2012). This is because mass effects cause an increase in the frequency of species outside their habitats which results in the weakening of the species-habitat relationship (Debinski et al. 2001). Ultimately, landscape connectivity and its effect on species turnover will vary according to the properties of the organisms and the features of the landscape (Tscharntke et al. 2012).

DISTURBANCE

Disturbance (e.g. forest fires, floods, a falling tree, grazing, etc.) has an important role in explaining the maintenance of patterns of species diversity (Cadotte 2007). Variation in the spatial and temporal distribution of disturbance generates a mosaic of patches in different successional stages, which positively affects species turnover (Hobbs and Huenneke 1992, Cadotte 2007, Limberger and Wickham 2012, Vanschoenwinkel et al. 2013). However, there have been many explanations about how disturbance operates. The frequency and intensity of disturbance are important factors when determining how disturbances will affect local communities (Hobbs and Huenneke 1992). At the same time, disturbances at the local scale interact with mechanisms at the regional scale (Vanschoenwinkel et al. 2013, Cornell and Harrison 2014). For instance, dispersal and disturbance are closely linked because the rate of dispersal from the regional species pool will determine the speed of recovery of a site after disturbance (Vanschoenwinkel et al. 2013). Such relationship between dispersal and disturbance can be linked with the competition-colonization trade-offs hypothesis that states that species that are very good at colonizing new patches are poor competitors. Dispersal would then allow these species to persist regionally even when they are out-competed from habitat patches (Skellam 1951, Levins and Culver 1971, Hastings 1980, Petraitis et al. 1989, Calcagno et al. 2006, Cadotte 2007). Hence, the interplay between the variation of disturbance in time and space with the competition-colonization trade-offs of the species in the regional species pool can promote species coexistence at larger spatial scales (Cadotte 2007).

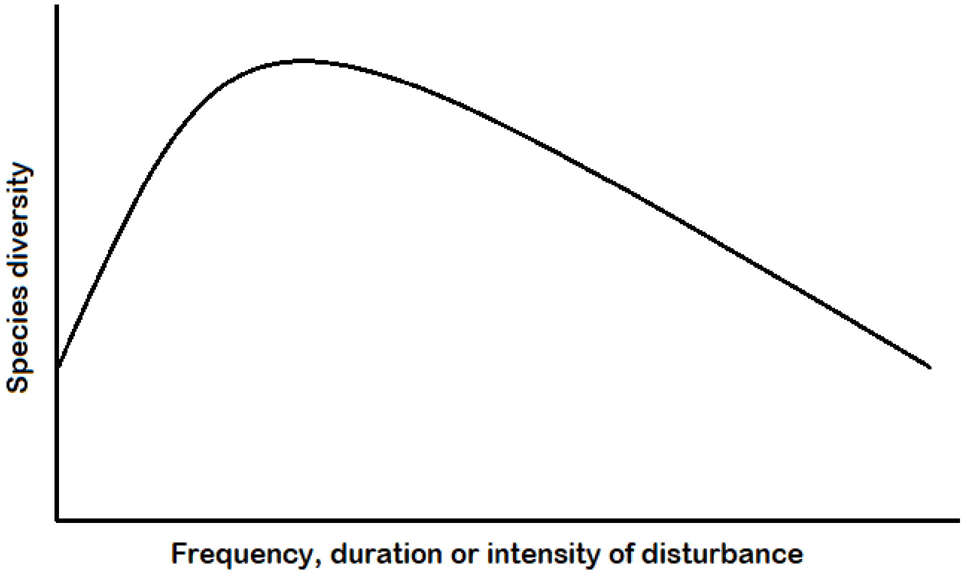

Figure 2. The intermediate disturbance hypothesis. Diversity will be at its maximum when the frequency of disturbance is intermediate. On the other hand, diversity will be low when the frequency of disturbance is low and when it is high (Adapted from Connell 1978).

The outcome in the local community can be regulated by the frequency of disturbance. The intermediate disturbance hypothesis argues that biodiversity will be highest at intermediate levels of disturbance (Figure 2; Connell 1978, Sousa 1979, Cadotte 2007). Even though the intermediate disturbance hypothesis has been highly debated because few empirical tests have supported it, disturbance and disturbance regimes are recognized as important mechanisms for maintenance of species diversity at larger spatial scales (Cadotte 2007). In frequently disturbed habitats, the competitive exclusion of species is delayed and extinction rates can exceed immigration rates, which create habitat patches under continuous colonization that are dominated by species that are good dispersers and disturbance tolerant species such as ruderal plant species. On the other hand, in an undisturbed habitat patch species that are long-lived and better at competing for resources will dominate. Thus, several species can survive if there are patches at different stages of recovery in the landscape (Hobbs and Huenneke 1992). As a result, species composition in areas that are subject to particular disturbance regimes will differ when compared to undisturbed areas, positively affecting species turnover (Petraitis et al. 1989). In general, species' response to disturbance can vary depending on the disturbance's frequency, intensity, extent and duration (Shea et al.

2004). For instance, intensively grazed pastures in a heterogeneous landscape had lower insect species richness compared to extensively grazed pastures (Kruess and Tscharntke 2002). The extent of the disturbance is an important factor affecting species turnover. Disturbances at a local scale generate mosaics of patches at different successional stages. On the other hand, large-scale disturbances such as hurricane damage or forest fires, can have a different effect on species turnover. In this case, regeneration succession occurs at the scale of disturbance and species turnover would be low (Maarel 1993).

IMPLICATIONS AND CONCLUSIONS

There is not one single mechanism determining the turnover of species among sites. It was evident throughout this essay that each mechanism has an effect on the composition of communities, but in itself is not enough to explain the causes of species turnover. Therefore, it may seem that what drives species turnover is a mishmash of interacting mechanisms at different spatial scales. However, the development of theoretical concepts such as the regional species pool, the fundamental and realized niche, connectivity, metapopulations and metacommunities, have aided our understanding of what drives species' distributions. The regional species pool concept is a good starting point. The effects of the regional species pool on local diversity depend on the structure of the landscape, the rate of dispersal of the species in the regional pool or on the rates of disturbance. Even though the regional species pool's own characteristics are essential, the filters that govern it can have a drastic effect on species turnover. The niche concept is useful to understand the effects of the abiotic and biotic filters and of environmental heterogeneity on species turnover. Each species has a fundamental niche as a response to a set of environmental conditions, and in a heterogeneous landscape where these conditions are fulfilled the species should theoretically be present. However, biotic interactions prevent the species to be present everywhere where the conditions are optimal (realized niche) which positively affects species turnover. The strength of the biotic interactions determines whether a local population is mostly dependent on local processes or on processes at larger spatial scales such as dispersal.

Dispersal effects on turnover can be either negative or positive depending on the landscape and on the rates of extinction and emigration. Additionally, the rate of dispersal within the regional species pool has an effect on species turnover. If the rate of dispersal is high, species turnover will be low because local communities will be similar to each other. But if the rate of dispersal is low, species will aggregate locally which will benefit species turnover. However, the capacity to disperse depends on the life history of the organism and on how the organism interacts with the surrounding landscape. At this point the concept of connectivity, both functional and structural, becomes relevant in order to be able to understand how the landscape influences the dispersal ability of different organisms. Dispersal is also closely related to the rate of disturbance because the rate of dispersal of the regional species pool will determine how fast a site can recover after a disturbance. The interplay between dispersal and disturbance allows for poor competitive species to survive in the landscape. However, the effect of the frequency, intensity, extent and duration of the disturbance is crucial on species turnover. In addition to this, there are several drivers of species turnover that have not been touched upon in this essay, such as stochasticity, speciation, selection, evolutionary and biogeographical history and time.

Another issue highlighted in the essay is spatial scale. The effects of the mentioned mechanisms are highly dependent on the spatial scale of observation. Environmental heterogeneity becomes relatively more important for species turnover at larger scales, while the importance of species interactions is most relevant at local scales. Furthermore, the scale at which organisms respond to the surrounding environment is relative to the properties or traits of the organism in question and their perception of the environment. Decisions to disperse can e.g. depend on the species' habitat requirements, the habitat patch's boundaries, or on the presence or absence of conspecifics. It is thus impossible to establish a scale at which all taxa can be studied because species turnover is affected by a myriad of mechanisms at different spatial scales. Therefore, if the aim of the study is to identify the scale that is relevant for a certain mechanism affecting turnover or to study the relevant mechanisms affecting turnover at a specific scale, one should always be aware of the relative importance each mechanism plays at the scale of observation. This is important in order to overcome empirical inconsistencies in the study of turnover in community composition

Land-use intensification and habitat loss are major drivers of biodiversity decline and homogenization of local communities across space (Tscharntke et al. 2012). In addition , global climate change is causing a shift on the climatic niche of species resulting in species with shifted distributions, phenologies and even shifted physiology (Bellard et al. 2012) . It is therefore crucial to understand how climate change interacts with the current landscapes and how it affects individual species distributions and dispersal and the interactions between them. Understanding the mechanisms that drive species turnover in space is critical for mitigating the effects of climate change and habitat loss. A starting point is to understand how local extinctions and the configuration of the landscape affect the regional species pools. Hillebrand et al. (2018) pointed out that local species richness rarely changes, and that we therefore need to look more closely into turnover of species between sites. The rates of immigration and extinction in a community are highly useful to determine the effects of ecosystem change on community composition. Therefore, future research should make use of species turnover metrics in combination with the theoretical concepts mentioned in this essay to better understand the effects of ecosystem change on biodiversity. It is of great importance to implement different theoretical concepts into the research of species turnover. The mentioned mechanisms plus evolutionary processes, biogeographical history, stochasticity among others all provide a valuable piece of information as to why a species is present or absent in a locality and can therefore help us to better understand the consequences of anthropogenic activities on biodiversity. Broadening our knowledge will allow us to better predict and prevent biodiversity loss and the loss of ecosystem services that accompanies it.

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