Applications of biodiversity theories in conservation

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Abstract

Biodiversity theories are not very often explicitly consulted in conservation practice, but implicitly many conservation decisions rely on theory. Biodiversity theories can inform important conservation actions such as assessments of species richness and extinction or habitat loss and fragmentation. Popular examples of biodiversity theories are niche theory and island biogeography theory, whereas neutral theory is less known. Here, we review the implications of biodiversity theories for conservation practice, focusing on neutral theory. Neutral theory assumes that the establishment and success of an individual in a community does not depend on its species identity, but is instead predominantly driven by a stochastic process. We found that drift and stochasticity appear much less frequently in conservation studies than selection processes typical of niche theory. This might be because habitat-specificity is not supported by neutral theory, but is common among rare and vulnerable species. Furthermore, neutral theory makes less intuitive assumptions than niche theory and does not consider trophic interactions. However, models based on neutral theory proved to be useful in some biodiversity hotspots. Moreover, some models based on neutral theory

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subdivide space into local community and metacommunity, which reflects concepts commonly used in conservation science. Neutral approaches have been used in conservation to generate realistic species-abundance distributions and species-area relationships, provide a standard against which to compare species loss, prioritize species protection, model biological invasions, and support protected area design. We propose that neutral theory can serve as a valuable first-order approximation to reduce complexity and by design account for drift and stochasticity. Neutral theory provides the benefits of a community theory whereas niche theory focuses on single species. Ideally, neutral approaches should be used as a starting point for conscious stepwise addition of niche structure. This step-wise approach reflects recent integrative biodiversity theories that combine aspects of neutral and niche theory such as the stochastic niche or emergent neutrality and may provide a promising foundation for future conservation practice.

Introduction

Conservation decisions are rarely explicitly based on theoretical considerations, but theory often implicitly influences the viewpoints that are adopted in conservation biology. Since biological diversity is the main target of conservation actions (Sutherland et al. 2009), theories on the mechanisms that maintain and enhance biodiversity are highly relevant to conservation. Indeed, niche theory (Tilman 1982) has been applied by conservation practitioners to delineate conservation areas (Eppink & van den Bergh 2007) or to manage invasive species (Caplat et al. 2013). Island biogeography theory (MacArthur & Wilson 1967) provides an important cornerstone for understanding the impacts of habitat loss and fragmentation (Laurance 2008). Together, niche theory and island biogeography theory have been considered very influential in the development of conservation concepts (Schulte et al. 2006). Another vein of biodiversity theories are neutral theories that assume that the establishment of individuals in a community does not depend on their species identity, but is mainly driven by stochastic processes such as demographic drift and sometimes stochastic dispersal and stochastic speciation. For instance, species-area-relationships may arise from neutral processes and many meta-community models used in conservation are essentially neutral when they ignore species interactions or species identities. Overall, there are only few conservation studies that explicitly refer to a biodiversity theory, especially when it comes to neutral theories. Therefore, in this paper, we review the applications of niche theories, neutral theories, and their mixtures in conservation. We particularly focus on the neutral theory by Hubbell (2001), because it has sparked controversy among ecologists (e.g. Ricklefs 2003; Nee 2005) and has not yet been discussed very much in conservation biology.

Biodiversity theories are very diverse. More than one hundred biodiversity-maintaining mechanisms have been proposed (Palmer 1994), which makes it difficult to identify the suitable theory for a specific conservation task. However, all established biodiversity theories are based on the presence or absence of four distinct processes: selection, ecological drift, speciation, and dispersal (Vellend 2010). Selection is the deterministic process that leads to the set of species present in a community after competitive, trophic, and mutualistic interactions with other species and interactions with the environment have taken place. In contrast, ecological drift covers all random processes that lead to survival or extinction of species within a community. Originally, niche theories have included selection, but not ecological drift (e.g. Tilman 1982), and sometimes speciation and dispersal (e.g. Ricklefs 1987), whereas neutral theories have included ecological drift and sometimes speciation and dispersal, but not selection (e.g. Hubbell 2001). Within this framework, MacArthur and Wilson's (1967) island biogeography theory involves the processes of drift and dispersal. It can thus also be considered neutral, but only at the level of species and not at the level of individuals as it is the case in Hubbell's (2001) neutral theory. More recently, intermediate biodiversity theories such as the stochastic niche theory (Tilman 2004), the continuum theory (Gravel et al. 2006) and the concept of emergent neutrality (Scheffer & van Nes 2006) incorporate both selection and ecological drift to varying degrees (Fig. 1).

Selection-focused theories such as classic niche theories (MacArthur 1972; Tilman 1982; Gause 2003) explain the coexistence and co-occurrence of species with differences between species that are relevant for their survival under environmental conditions that vary in space and time. Each species has a specific ecological niche, i.e. a set of conditions to which it is better adapted than all of its competitors with regard to environmental conditions, predators and other antagonists. For conservation, this implies that species are not easily interchangeable. To a certain degree, this justifies the protection of every single species including flagship species, challenges insurance effects, and calls for the combat of invasive species (Table 1). However, since species can differ in many different traits, selection- or niche-based explanations of biodiversity often come with the disadvantage of increased complexity (Rosindell et al. 2011).

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Complexity of niche structure can be a disadvantage for three reasons: If the complexity is not entirely justified by the structure of the targeted community, first, too complex or generally unsuitable conservation actions might be devised, and second, the explanation will not be parsimonious, i.e. not fulfill the scientific claim to search the simplest possible explanation. Third, if the community is complex enough to justify multi-dimensional niche structure, it might be challenging to derive the corresponding conservation actions.

Drift-based theories such as Hubbell’s (2001) neutral theory, in contrast, make fewer assumptions. Hubbell’s (2001) neutral theory assumes that differences between species of the same trophic level are irrelevant for demographic rates. Independent of species identity, individuals are equivalent in their fitness with respect to birth and death rates or dispersal ability. This is also summarized as ecological equivalence (Munoz & Huneman 2016). For instance, a tropical tree species is typically surrounded by many different tree species. This prevents specialization on interactions with a particular species leading to generalist strategies and thus quasi-equivalency on evolutionary time scales (Hubbell 2006). In a neutral framework, the probability of a species to establish in an available habitat patch in a local community predominantly depends on its frequency in the local community and not on how well it might be adapted to the environmental conditions in the habitat patch (Purves & Pacala 2005). Additionally, in Hubbell’s (2001) neutral theory, there is a small probability that a species that is not present in the local community establishes in the available habitat patch by dispersal from the meta-community or by speciation. Lacking differences in demographic rates, all species in a neutral community would be interchangeable at any time (Purves & Pacala 2005) without destabilizing the local community. Recently, the realism of key parameters and outputs of the neutral theory have been improved, for instance with respect to the size of the local community (Richardson, Barry J.; Arias-Bohart 2011), species age (Chisholm & O'Dwyer 2014), and spatial structure (Rosindell & Cornell 2013). Including spatial structure into drift-based theories is important for discussions in conservation biology on meta-communities and habitat fragmentation.

Drift-based applications in conservation highlight the role of stochasticity for biodiversity maintenance and usually have straightforward mathematical solutions (Rosindell et al. 2012). Considering drift and ecological equivalence may be relevant whenever species show large niche overlap or are not very habitat-specific. We are aware that many species of conservation concern show high habitat-specificity (e.g. Goerck 1997). Therefore, drift-based theories have limited applicability to communities with these species. However, for the remaining communities such as tropical tree communities in Panama (Hubbell 2005), drift-based neutral approaches could be valuable alternatives to selection- and niche-based approaches. With respect to conservation management and ignoring intrinsic or utility values of species, protection of single species would only be necessary to the degree to which ecological equivalence can be rejected (Table 1). Where there is evidence for strong ecological equivalence, the protection of species richness in terms of species numbers, not species identities or niches, will suffice to maintain community stability. In these cases (and only if intrinsic or utility values of species are ignored), the most intuitive unit for conservation actions would be the whole community and its ecosystem processes rather than populations or species.

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Validation of biodiversity theories against real-world data is necessary to assess the practical importance of selection and drift in a given conservation framework. Validation has most commonly been attempted with rank-abundance distributions. Empirical rank-abundance distributions were successfully reproduced by the neutral theory for a range of ecosystems, such as tropical rainforests in Panama (Hubbell 2001), tropical freshwater fish communities (Etienne & Olff 2005), and partly microbial communities in waste water treatment plants (Ofiteru et al. 2010). Niche processes were for instance shown to predominate for a coral reef community (Dornelas et al. 2006; but see Volkov et al. 2007 for a neutral coral community) and a salt meadow community (Anderson & Mouillot 2007). Neutrality has been reported more commonly from productive environments such as tropical forests, whereas niche structure seems to be more important in less productive systems such as temperate forests or grasslands (Chase 2010). Species-rich communities are of particular conservation concern. They often exhibit strong recruitment limitation, which can prevent competitive exclusion, thus promoting de facto neutrality. This has for instance been shown in a tropical rainforest (Hubbell 2006) and a fynbos shrub community (Perry et al. 2009). Originally, neutrality was suggested to be applicable at larger spatial scales than niche theory (Bell 2001), but recently niche structure has been shown for large scales, too (Tang & Zhou 2011), and niche and neutral processes have been considered difficult to distinguish at small and intermediate scales (Gilbert & Lechowicz 2004). This underlines the importance of considering both niche and neutrality especially at the local scales at which most conservation efforts operate.

In the following, we will first briefly summarize conservation implications of selection-based niche theories as a reference standard for comparisons. We will then compile case studies addressing Hubbell's (2001) neutral theory as an example of a drift-based approach in two categories, i.e. (i) only implicit conclusions for conservation efforts can be drawn and (ii) explicit conservation conclusions are drawn in the study. Finally, we will synthesize our findings by evaluating the beneficial and detrimental consequences of drift-based approaches such as the neutral theory for conservation and highlighting the implications of current developments in biodiversity theory for conservation.

Survey Methodology

We searched the Web of Science for papers published between 2001 and July 2018 to obtain a sample of studies linking neutral theory and nature conservation (see Appendix S1 for a documentation of search terms). To be included in this review, a publication had to match one of the following criteria: i) It had to address a link between niche theory and conservation; ii) it had to introduce a new approach based on neutral theory, which could theoretically be applied in conservation; or iii) it had to address an already established approach for the application of neutral theory in conservation (see Appendix S2 for time series of publication counts for different search terms). Although we have considered any theory that was named "neutral" in our query, a focus on Hubbell's (2001) neutral theory emerged from the search, because it was by far the most commonly mentioned neutral theory.

Selection-based niche theory and conservation

The niche concept is firmly established as a basis for decision-making in modern nature conservation. A majority of nature conservation studies therefore implicitly or explicitly refer to the niche concept and its derivations. As explicit examples, ecological niche models have been used for the delineation of conservation areas (Eppink & van den Bergh 2007; Girardello et al. 2009; Cianfrani et al. 2013; Mateo et al. 2015), the assessment of habitat loss (Barrows et al. 2008, 2011), and invasive species management (Caplat et al. 2013; Vicente et al. 2013; Guisan et al. 2014; Thalmann et al. 2015).

Ecological niche modeling

Ecological niche modeling is widely used to predict potential distributions of organisms in space (Giovanelli et al. 2008; Murray et al. 2011; Vasconcelos et al. 2012). Niche models provide guidelines for the selection of conservation areas and future strategies in conservation planning (e.g. Vega Rivera et al. 2011; Tobler & Morehouse 2013). Beyond theoretical use, niche models are focused on explicit locations and landscapes (Girardello et al. 2009). This spatial context can for example help to evaluate the range in which a species is protected by current conservation areas (Ochoa-Ochoa et al. 2009) or to identify priority areas for future conservation reserves, even without empirical data on species distributions in these areas (Ortiz-Martínez et al. 2008). Niche models are particularly useful under current climate change, because they can provide predictions of species responses to future environmental variation (Kleinbauer et al. 2010).

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These predictions may lead to the modification of current conservation programs or the establishment of new conservation actions.

Habitat loss and habitat fragmentation

Habitat loss can only be critically assessed under the consideration of former geographical distributions of species. This can be estimated by niche models combined with abiotic variables that are independent of anthropogenic influence (Barrows et al. 2008; Escobar et al. 2015). These historical distributions can further be used to locate suitable areas for restoration and reintroduction of species (Barrows et al. 2008). Habitat loss often leads to habitat fragmentation that can reduce viability of the species in a community. Therefore, a core objective of biological conservation is to maintain linkages between habitats, such as in the form of habitat corridors. Again, niche models have been used to identify pertinent linkages, which can then be proposed as conversation areas (Barrows et al. 2011).

Invasive species

Niche-related analyses also estimate the hypothetical distribution of non-native invasive species (Peterson & Robins 2003; Giovanelli et al. 2008; Kleinbauer et al. 2010; Murray et al. 2011). A common output is the determination of containment boundaries for ecological threats to local communities (e.g. Giovanelli et al. 2008; Murray et al. 2011). Furthermore, the results of niche-based analyses have been used to derive invasion potentials and to explain why species can invade new communities (Murray et al. 2011; Tobler & Morehouse 2013).

Neutral theory with implicit conservation implications

Neutral models, which implement neutral theory by involving different degrees of drift and stochasticity, have generally been used to answer questions on species richness and extinction at different spatio-temporal scales (Adler & Muller-Landau 2005; Babak & He 2009; Dornelas 2010). Neutral models have also been developed to compare the effects of different levels of ecological disturbance on species richness and abundances (Bell 2000; Kadmon & Benjamini 2006). This is particularly important if the conservation target is to preserve the current community composition, because these models might show whether and how disturbances alter current community composition. Such insights should be considered in the design of the corresponding conservation actions.

Meta-community dynamics have recently found entrance to nature conservation studies (Gimona et al. 2012; Diaz et al. 2013). Neutral theory-derived models can be used for explorations of meta-community theory, because of the appropriate representation of species, and especially of rare species, in neutral theory (Driscoll & Lindenmayer 2009) and the recent advances in spatially-explicit implementations of neutral models (e.g. Rosindell & Cornell 2013).

Spatially-explicit versions of the neutral theory have proven their ability to explain spatial patterns in several studies (e.g. Gardner & Engelhardt 2008; Yakimov et al. 2014). For instance, Gardner and Engelhardt (2008) developed a spatially explicit neutral simulation model of a plant community to reduce the initially high dimensionality of the study. Their neutral model showed that population establishment depended on long-distance dispersal, but population persistence on aggregated spatial distributions of species. For desired species, the potential conservation implication of this study would be to increase landscape conductivity to promote long-distance dispersal and to preserve areas for species aggregates. In general, predictions from spatial neutral models can thus easily be applied to real landscapes, which can simplify conservation efforts.

Neutral theory with explicit conservation implications

Explicit conservation implications are formulated only in a few studies that address neutral theory or neutral models. These studies aim to delineate protected areas, approximate species richness measures and predict extinction rates.

Habitat fragmentation and protected areas

A major concern of conservation is habitat fragmentation, since it is one of the primary causes of species loss (Tilman et al. 2001; Rands et al. 2010). However, only few studies link habitat fragmentation and neutral theory. In one of these studies, Babak & He (2008) investigated habitat fragmentation impacts on species diversity with a neutral simulation model for species abundance dynamics in two local communities. These two local communities are connected to a regional meta-community. In essence, this is similar to a source-sink meta-population approach where the subpopulation dynamics rely on drift. In this neutral simulation model, migration between local communities leads to a homogenization of community composition, whereas immigration from the meta-community into local communities causes community differentiation. Hence, the size of spatial habitat fragments mattered for biodiversity, calling for a conservation strategy implementing “several small” reserves rather than one “single large” reserve (see SLOSS debate, Simberloff & Abele 1976). With a similar spatial neutral modelling approach, Economo & Keitt (2010) found that geographic isolation reduces biodiversity only at certain critical scales that depend on the relative rates of dispersal and evolution in the model. Based on results from a spatial neutral meta-community model, Economo (2011) further suggests that protected areas rather than biodiversity representation should be maximized to achieve long-term biodiversity conservation.

Biodiversity and extinction

Biodiversity is a major concern for conservation efforts, first because it is considered of value in itself, second because it often is the basis for ecosystem functioning (Hooper et al. 2005). Tropical rain forests are hotspots of biodiversity with a distribution that has a long tail of rare species, which can be described by the neutral theory (Hubbell 2001). Similarly, urban soil mite biodiversity has successfully been described with stochastic models based on neutral theory (Caruso et al. 2017). Furthermore, Hubbell (2013) identified the linkage between absolute abundance and geographic range of species as fundamental for conservation in tropical regions. For instance, Hubbell et al. (2008) were able to estimate stand characteristics such as number, relative abundance and range size for trees in an Amazonian meta-community by implementing neutral assumptions. They predicted the rate of extinction for overall species numbers under different scenarios. Similarly, Chisholm et al. (2018) used neutral models to place upper and lower bounds on species loss with respect to different degrees of habitat destruction. Hence, if neutral models generate realistic range distributions and species abundance distributions, they can not only deliver a quantification of species extinctions to conservation practitioners, but also inform strategies to combat species extinctions. Such a neutral theory-derived strategy would be to preserve stochastic processes and especially environmental stochasticity (Danino et al. 2016) in protected areas instead of single species protection (Table 1). However, caution needs to be taken, because the same community-level pattern can result from different mechanisms, so alternative theories about the mechanisms need to be ruled out, before such a strategy is implemented. Furthermore, species vulnerability has been assessed for several global change scenarios by analyzing the degree of connectivity for estuarine communities along the Iberian coast (Chust et al. 2013). By combining these correlative analyses with neutral theory, a prioritization of the most vulnerable species and habitats for conservation plans was achieved. Neutral theory has also been used to construct null models as a standard for comparisons of plant and insect species loss under land-use change (Uchida et al. 2016) and to determine extinction risk under yearly or decadal climate changes (Fung et al. 2016). Halley et al. (2014) provide a framework based on neutral theory linked to species area-relationships that can be used to evaluate results from extinction forecasts or simulated habitat contractions. Their work improves the distinction between imminent and delayed extinction debts by clarifying the relationship between extinction debt and species-area relationships. Where neutral theory applies, this framework can highlight the driving forces of extinction processes in small remnant areas and can be used to define area requirements of species and communities as a basis for planning protected areas.

Invasive species

Habitats that are more prone to species invasion are often created by stochastic disturbances (Daehler 2003; Davis et al. 2005) promoting drift processes. This calls for including stochasticity into ecological models of community dynamics. In their review of invasion of natural communities by alien species, Daleo et al. (2009) highlighted this need of including stochasticity in models of community structure. They emphasize that biological invasions and the ecological patterns that arise from invasions indicate that trait differences between species are not necessarily the only drivers of ecological patterns. Therefore, conservation research should consider stochastic processes and drift. Note that whereas stochasticity and drift are by definition included in neutral theory, they can also be included in niche theory. Including stochasticity in invasion models has been shown to be justified: Herben (2009) observed broad agreement between the predictions of a simple neutral model with observations from field studies with respect to invasion patterns, such as i) enhanced community invasibility after disturbance, ii) positive relationship between residence time of invasive species and success of invasion, iii) constant ratio of successful invasive species, and iv) higher growth rates of invasive species in comparison to native species. Neutral theory, therefore, seems capable of elucidating invasion processes and provides tools for conservation cases that do not require species-specific assumptions. In those cases, invasion would only require conservation intervention if there are marked effects on the whole community and not only one native species is replaced by one invasive species (Table 1).

Discussion

Neutral and niche theories of biodiversity (or drift- and selection-based approaches) are complementary in their consequences for conservation, especially with respect to species conservation. A niche perspective leads to a focus on interactions of species with the environment and with other species. Neutral approaches ignore such interactions and highlight similarities between species and the influence of stochastic processes. In strongly niche-structured communities, protection of single species and niches as well as eradication of invasive species can be justified. In communities where drift and stochasticity are important, neutral approaches add weight to the argument of conservation practitioners to protect communities, processes and areas instead of single species. Invasive species would be treated as any other species in a community, since all individuals, and thus all species, are ecologically equivalent in neutral theory (Hubbell 2001).

Neutral and niche theories have similar fields of application in conservation, but show great differences in their frequency of application. We found that niche theory still is the main theory driving conservation decisions. For instance, niche modelling is a very common technique and has been applied to plan protected areas, assess habitat fragmentation and derive invasion potential of exotic species. Contrastingly, our review shows that approaches based on neutral theory have found much fewer explicit uses in conservation applications. Implicit applications of neutral assumptions can be found in several conservation contexts including stochastic disturbances or addressing meta-communities with many rare species. Explicit applications of neutral theory have dealt with species-abundance distributions, species-area relationships, habitat fragmentation, invasion patterns and extinction probabilities. Analogous to the heated debates that have accompanied the publication of the neutral theory (e.g. Ricklefs 2003, 2006), considering neutral theory in the context of conservation has its benefits and caveats.

One of the benefits of neutral theory and drift-based approaches in general is that they promote an explicit consideration of stochasticity (Alonso et al. 2006) at the level of populations (reproduction, mortality) and communities (colonization, speciation; Fig. 2). This mirrors the awareness of conservation biology that stochasticity, such as in the form of demographic stochasticity (Lee et al. 2011), environmental stochasticity (Stacey & Taper 1992), or random catastrophes (Lande 1993) can have huge impacts on species extinctions and community composition. The focus of neutral theory on individuals and abundances may at first glance differ from the traditional focus of conservation biology on species. However, individuals are important in conservation biology: single individuals start an invasion, make up the small populations of rare species, are the level of natural selection or use wildlife bridges and connect populations. Moreover, whenever knowledge about species traits is sparse, assuming ecological equivalence of species, at least as a first step, might be more suitable than making arbitrary assumptions about trait values (Rosindell et al. 2012) (Fig. 2). Neutral theory, especially in its spatially-explicit versions, also highlights the importance of spatial processes such as dispersal and can predict reliable species-area relationships (Rosindell & Cornell 2007), which are so important for conservation. In conservation, spatial relationships play an important role, for instance in the context of delineation of protected areas (Patiño et al. 2014), connectivity of meta-populations and meta-communities, and habitat fragmentation. It is thus not surprising that Holt (2006) declares the neutral theory as crucial for understanding fundamental processes of community ecology and applying this understanding to conservation issues.

One disadvantage in applied contexts of neutral theory is that disregarding conspicuous differences between species has proven counterintuitive to many ecologists and conservationists. In contrast, niches are an appealing concept, because they explain community assembly based on the observable species differences. Hence, conclusions drawn on the basis of models based on neutral theory may be less acceptable to stakeholders and conservation funders than those based on niches. This should not be used as an argument against the application of neutral models in itself, but may be one reason for the fact that we found only few explicit neutral theory-related studies in the context of conservation biology. Another reason might be the *de facto* limited range of application of Hubbell's neutral theory to sessile organisms within the same trophic level in homogeneous areas (for one of the very few exceptions see Ofiteru et al. 2010). Consequently, in their compilation of the influential ecological theories with respect to forest biodiversity conservation, Schulte et al. (2006) list niche theory and island biogeography theory, but not Hubbell's neutral theory. Clark (2009) cautions against the loss of process knowledge should neutral theory be adopted in biodiversity science. Based on these arguments, there are claims to call the applicability of neutral theory to conservation contexts entirely into question (e.g. Clark 2009; Bode et al. 2012). We argue, however, that the fact that neutral theory applies only to some and not all cases should not result in a blanket ban of the theory. We rather advocate a conscious choice and mix of drift and selection, based on the degree to which assumptions of the one or other theory are fulfilled.

Theory in general may also be considered a source of confusion in normative conservation practice, because theory often is perceived to be abstract, complex, and only accessible to theoreticians. This applies to all biodiversity theories, not only the neutral theory. According to Driscoll & Lindenmayer (2012), this confusion can be overcome if the predictive capacity of theory is better delineated, so that appropriate conservation applications can be identified. Here, both the simple assumptions and the limited, but clear set of possible predictions of neutral theory are advantageous. Thus, neutral theory can serve as a null model or a first-order approximation with the chance to “fail in informative ways” (Rosindell et al. 2011). Such an informative failure can lead to the successive addition of more assumptions, such as in the form of different degrees of niche structure, until realistic patterns are produced. More complex models can thus be deduced from neutral theory as a starting point (Fig. 2). Conservation can benefit indirectly (dashed arrow in Fig. 2) from such applications of neutral theory if they lead to more accurate models for the projection of population and community dynamics. This approach also changes the point of view from an unquestioned niche perspective to a conscious and parsimonious choice of the amount of niche structure that is necessary to describe a given community. Thus, theory can be of great benefit to conservation if it is well defined and can flexibly be adapted to the case at hand.

Integrative biodiversity theories that accommodate both neutral and niche processes at variable proportions comply with Bode et al.'s (2012) call for new ecological theories that can better inform conservation (Fig. 2). Based on their study of species-area relationships as a basis of protected area design, Patiño et al. (2014) argue that rather than relying on a single framework that includes either niche or neutral parameters, the focus should shift further to integrative approaches that take advantage of both theories. Attempts to integrate niche and neutral processes into a single framework include stochastic niche theory (Tilman 2004), continuum theory (Gravel et al. 2006), a generalized neutral theory including environmental stochasticity (Bewick et al. 2015; Kalyuzhny et al. 2015) and a mathematical blend of both concepts (Noble & Fagan 2015), as well as the rising concept of emergent neutrality (e.g. Holt 2006). For instance, Noble & Fagan (2015) explicitly highlight the capacity of their blended model to quantify the impact of forces that stabilize or destabilize niches on population extinction times. Niche theory states that species need to be sufficiently different to coexist. Emergent neutrality additionally predicts that at evolutionary time scales, the opposing effects of habitat filtering and niche differentiation lead to the coexistence of ecologically similar species, resulting in effective ecological equivalence (Carmel et al. 2017; Scheffer & van Nes 2006). The progress in these hybrid models revealed the necessity of including further factors beyond those covered by niche or neutral theory alone (Kalyuzhny et al. 2014). This as well as generally considering more theory in conservation would advance the understanding of the dynamic properties of communities, which is of crucial importance for conservation decision-making.

In conclusion, neutral approaches have thus far been used in only few conservation studies compared to the popularity of niche-based approaches. However, this does not always reflect factual restrictions in the applicability of one or the other approach to a certain conservation question. Therefore, it seems prudent to open-mindedly consider both niches and neutrality in models and concepts that are intended to inform conservation actions. Such integrative models may start with purely neutral dynamics, especially but not only where stochasticity is known to be important, where communities are in the focus rather than single species, or where data on species properties are scarce. Then, adjustable levels of niche structure are added until differences between model output and reality are minimized (e.g. Buschke et al. 2016). This shift of perspective towards approaches that unify niche and neutral views has been very much supported recently (Matthews & Whittaker 2014). Overall, conservation practitioners and ecologists should thus work towards identifying and applying the suitable mix of neutrality and niche for their particular cases as a basis for successful future conservation.

Supporting Information

A table with search terms (Appendix S1) and figures with time series of paper counts (Appendix S2) are available online. The authors are solely responsible for the content and functionality of

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these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1: Conservation actions in the form of questions for drift-dominated and selection-dominated communities (Communities A and B in Fig. 1) when the conservation target is to protect biological diversity and intrinsic or utility values of species are ignored. Drift is the core process in neutral theory whereas selection is central to niche theory.

Conservation action	**Drift-dominated community (A)**	**Selection-dominated community (B)**
● Should particular species, i.e. species identities (including flagship species), be protected?	No, since all species are equivalent	Yes, because differences in species identities matter for establishment and survival
● Should species richness, i.e. number of species, be protected, regardless of species identity?	Yes, because large communities usually are more stable than small communities (e.g. Brose et al. 2006)	No, species identity should also be considered
● Should protection focus **more** on areas than on community composition, i.e. species identities?	Yes, because protected areas protect the ecological processes within a community, including drift	No, even though protected areas can of course be a highly effective means to protect species identities
● Should rare species receive special attention?	No, even if rare species go extinct, they will eventually be replaced by an equivalent species via drift	Yes, because they are not replaceable once extinct
● Should an invasive species that replaces a single local species be combatted?	No, because all species are equivalent (yes, if we target global species richness and a local endemic is lost)	Yes, because species identities are not replaceable
● Should an invasive species that reduces local species richness be combatted?	Yes, because large communities usually are more stable than small communities (e.g. Brose et al. 2006)	Yes, because species identities are not replaceable

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Figure legends

Figure 1: Communities are shaped to different degrees by drift and selection processes. Community A represents a community that is dominated by drift processes and community B a niche-structured community where selection processes dominate. Neutral communities often are species-rich (Hubbell 2006), but not very large in terms of individuals (Vellend 2010), whereas niche-structured communities are often large communities with few species (but the reverse does also occur). Disturbances can lead to declines in community size and enhance drift processes (Vellend 2010), whereas extinction and dispersal can reduce species richness and thus probably increase the importance of selection and niche processes.

Figure 2: The neutral theory of biodiversity can affect conservation directly (solid arrows) and indirectly via its influence on the scientific community and on modelling practice (dashed arrows).

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Figure 1

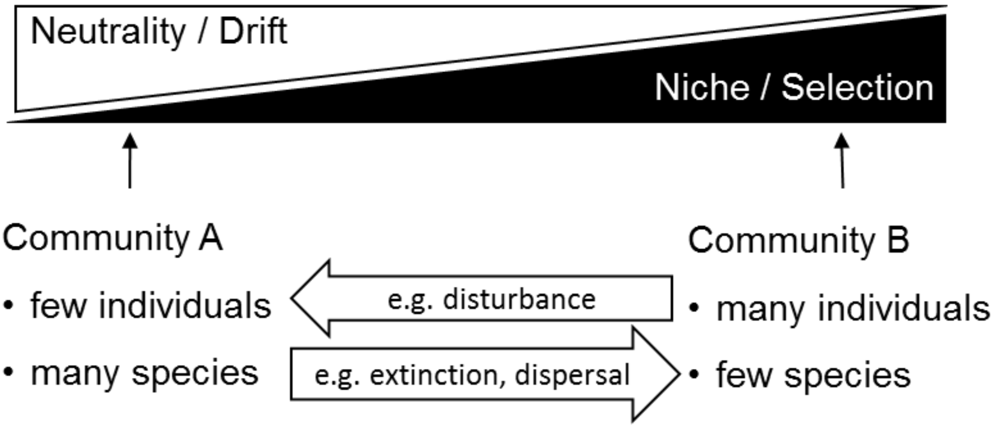
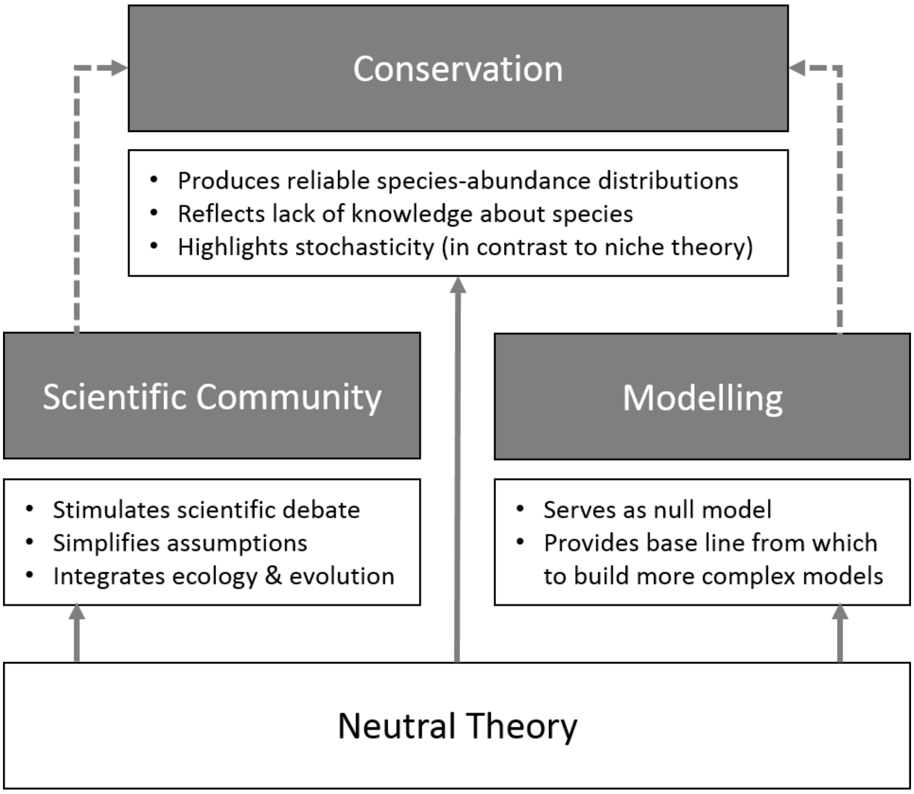

Neutrality / Drift
Niche / Selection
Community A
• few individuals
• many species
e.g. disturbance
e.g. extinction, dispersal
Community B
• many individuals
• few species

Figure 2:



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