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SYNTHESIS

The ecological causes of functional distinctiveness in communities

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Abstract

Recent work has shown that evaluating functional trait distinctiveness, the average trait distance of a species to other species in a community offers promising insights into biodiversity dynamics and ecosystem functioning. However, the ecological mechanisms underlying the emergence and persistence of functionally distinct species are poorly understood. Here, we address the issue by considering a heterogeneous fitness landscape whereby functional dimensions encompass peaks representing trait combinations yielding positive population growth rates in a community. We identify four ecological cases contributing to the emergence and persistence of functionally distinct species. First, environmental heterogeneity or alternative phenotypic designs can drive positive population growth of

functionally distinct species. Second, sink populations with negative population growth can deviate from local fitness peaks and be functionally distinct. Third, species found at the margin of the fitness landscape can persist but be functionally distinct. Fourth, biotic interactions (positive or negative) can dynamically alter the fitness landscape. We offer examples of these four cases and guidelines to distinguish between them. In addition to these deterministic processes, we explore how stochastic dispersal limitation can yield functional distinctiveness. Our framework offers a novel perspective on the relationship between fitness landscape heterogeneity and the functional composition of ecological assemblages.

KEYWORDS
coexistence, community assembly, ecological interactions, fitness landscape, functional traits, source-sink dynamics

INTRODUCTION

The factors driving the emergence and persistence of diverse phenotypes have long fascinated ecologists and evolutionary biologists (e.g. Darwin, 1859; Ewens, 1969). Functional distinctiveness measures the functional distance of a species to the other species in a community, with functionally distinct species being those farther apart from other species in trait space. Although these species can play critical roles in biodiversity dynamics, ecosystem functioning and stability (Auber et al., 2022; Brun et al., 2022; Dee et al., 2019; Delalandre et al., 2022; Le Bagousse-Pinguet et al., 2021; Violle et al., 2017), ecology has historically focused on the role that average phenotypes play in communities (i.e. species with low functional distinctiveness, or close to other species in trait space). To better understand and acknowledge the ecological significance of functionally distinct species, a comprehensive framework is needed to pinpoint the various ecological mechanisms that can allow these species to establish and persist in communities and ecosystems.

Here, we build a conceptual framework that encompasses the major ecological drivers of functional distinctiveness to help organize and inspire work in this emerging area. As a foundation of the framework, we adopt a widespread conception of biodiversity dynamics in which a regional pool of organisms influences local community composition (Cornell & Harrison, 2014; Denelle et al., 2019; Keddy & Laughlin, 2021; Koffel et al., 2022; Ricklefs, 2008). As such, a species that is functionally distinct in one community may not be distinct in other communities where it occurs. In the context of dynamic community assembly (Fukami, 2010; Weiher & Keddy, 2001), niche-based processes such as competitive exclusion and environmental filtering are often invoked to explain the local successes or failures of species that disperse from a larger species pool (Hubbell, 2001; Leibold et al., 2004). Depending on these processes, differential rates of growth, survival and reproduction represent fitness differences among coexisting species determining their establishment and persistence in communities (Laughlin & Messier, 2015). Therefore, the connections between traits, fitness variation, regional context and niche-based processes are an essential starting point for understanding the emergence and persistence of functionally more distinct species within communities. The framework we develop below offers a concise way to identify and test the range of purported ecological mechanisms for the origin and persistence of functionally more distinct species in communities. Our framework can then better incorporate insights from functional distinctiveness into ecology and conservation.

FUNCTIONAL DISTINCTIVENESS THROUGH THE LENS OF THE FITNESS LANDSCAPE

Introducing the fitness landscape

The foundation of our framework is the fitness landscape, first introduced in evolutionary biology (Wright, 1932), which is central to trait-based eco-evolutionary models (reviewed in Klausmeier et al., 2020). In this approach, a population's growth rate depends on the functional trait values that determine its phenotype in a particular environment. We rooted our framework on a generalized Lotka-Volterra competition model (Equation 1):

$$\frac{dN_i}{dt} = \left(r(\vec{x}_i) - \sum_{j=1}^{N} \alpha(\vec{x}_i, \vec{x}_j) N_j - \alpha_{\text{self},i} N_i\right) N_i \quad (1)$$

with population abundance N_i and trait vector $\vec{x}_i$ for each species $1 \leq i \leq N$. Here for simplicity of presentation, we ignored intraspecific trait variation. The function $\alpha(\vec{x}_i, \vec{x}_j)$ captures trait-dependent inter- and intra-specific interactions, and the $\alpha_{\text{self},i}$ term models species-specific self-limitation processes (Scheffer & van Nes, 2006).

Of particular importance is the intrinsic fitness landscape, given by the population growth rate in the absence of competitors $r(\vec{x}_i)$ (Figure 1b). A positive intrinsic growth rate means a species can establish itself in a local environment (see review by Klausmeier et al., 2020). The functional dimensions along which intrinsic growth rates vary reflect how species traits affect local demography (Kandlikar et al., 2022; Laughlin et al., 2020; Wright

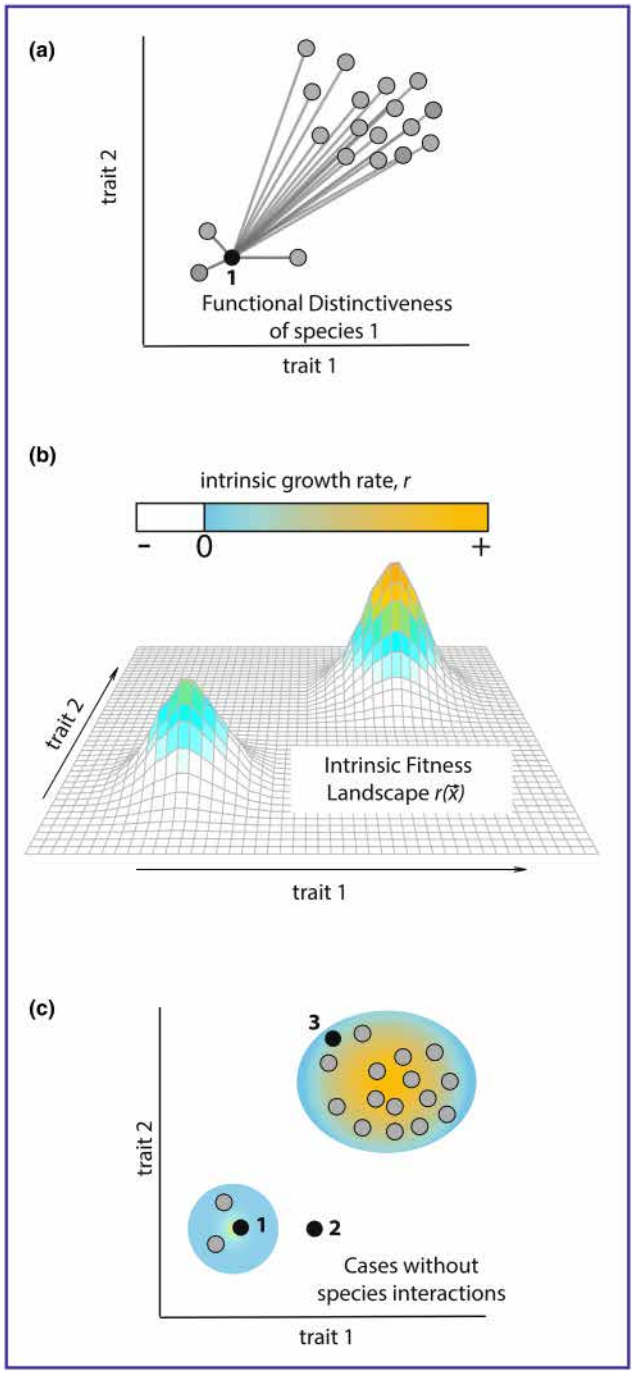

FIGURE 1 Influence of abiotic environment on functional distinctiveness through the intrinsic fitness landscape. Functional distinctiveness of a species in a community can be calculated as the mean functional distance to all the other species in the community (Panel a). The intrinsic fitness landscape can be constructed by representing how intrinsic growth varies with traits in the local environment (Panel b). Shaded areas on the peaks represent cases where intrinsic growth rates are positive ($r > 0$). Combining these perspectives, we can see that species (shown as points) may be functionally distinct for various reasons within the same community (Panel c). Three species are labelled corresponding to cases 1–3 in Table 1: species 1 occupies a distinct peak in a heterogeneous fitness landscape; species 2 represents a spatial or temporal sink population; species 3 is found at the margin of the main fitness peak.

et al., 2010), and these dimensions can be used to construct trait-fitness landscapes for any focal community.

Historically, community ecology has assumed that trait-performance relationships are unimodal, centred on a local trait optimum dictated by abiotic conditions (e.g. Davis & Shaw, 2001; Denelle et al., 2019; Whittaker et al., 1973). Here, we also incorporate the alternative - a fitness landscape that can be multimodal, including separate peaks of varying width and height (e.g. Whitlock et al., 1995) (Figure 1b).

We identified four potential ecological causes of the emergence and persistence of functionally more distinct species in local communities, depending on the topography of the fitness landscape. in the absence ($\alpha(\vec{x}_i, \vec{x}_j) = 0$, cases 1 to 3, Figure 1c) or presence ($\alpha(\vec{x}_i, \vec{x}_j) \neq 0$, case 4) of interspecific interactions (Table 1). In case 1, a few functionally distinct species can occupy a remote fitness peak in the landscape. In case 2, the environment is variable in space or time and entails source-sink population dynamics, and in case 3 the strategy is less fit (but viable) at the margin of a peak and thus less frequent in the local environment. These cases centre on the relationship between a focal species' population and abiotic environment through the intrinsic fitness landscape, which can be viewed as influenced by environmental filtering (Kraft, Adler, et al., 2015; Van Der Valk, 1981). Figures 1–3 are conceptual figures illustrating the fitness landscape framework and Cases 1–3. Case 4 represents how functionally distinct species can arise from biotic interactions with other species in the community. Figure 4 illustrates case 4 based on mathematical simulations. Apart from the four fitness-dependent cases, we expose how neutral stochastic dynamics (Vellend, 2016) can generate functional distinctiveness in a community, which can provide a null reference (Box 1).

Case 1: Local adaptation in a multimodal intrinsic fitness landscape

Given our understanding of the nature of trait space occupancy for many clades (Carmona et al., 2021; Díaz et al., 2016; Mouillot et al., 2021; Pigot et al., 2020), some trait-performance relationships can be multimodal, either globally or within local communities, despite a historical emphasis on unimodal relationships. Such multimodality translates into peaks in the intrinsic fitness landscape (Figure 1) and may arise for several reasons. First, there might be a multimodal spectrum of resources (e.g. small and large seeds that birds with different-sized beaks specialize in) (MacArthur, 1970; Ranjan & Klausmeier, 2022). Second, localities may be abiotically heterogeneous, comprised of microsites that vary in resources or stressors (Antonovics et al., 1971; Gram et al., 2004), microclimates (Baraloto & Couteron, 2010; Weiss et al., 1988; Zellweger et al., 2020), or disturbance regimes (Martinez-Ramos et al., 1988). This environmental singularity within a

TABLE 1 Causes of functional distinctiveness in ecological communities, with suggested diagnostics for assessing each cause in terms of a fitness landscape framework (Figure 1) and examples of the phenomena from existing ecological concepts or theories.

Case	Examples from existing concepts or theories	Underlying mechanisms	Patterns and dynamics of distinct species
Occupancy of distinct peak in a heterogeneous fitness landscape (Case 1)	Microhabitat specialization within a community; local adaptation	Distinct species exhibit positive population growth rates and occupy an isolated peak of the fitness landscape	Functionally distinct species are isolated in phenotypic space and are steadily present in the community over time
Spatial sink population (Case 2A)	Mass effects, source-sink dynamics	Distinct species are found in a local community where their fitness is negative, while they have high fitness in communities connected by dispersal	Functionally distinct species are steadily present in source communities and infrequently present in sink communities
Temporal sink population (Case 2B)	Storage effects; shifting baselines; paleoendemism	Local fitness landscape changed over time, so that species had higher fitness in the past, and are distinct with negative population growth rate currently	Functionally distinct species were more frequent in the past than nowadays, and they could be less distinct in the past
Species found at the margin of fitness surface (Case 3)	Constraints on adaptation; biophysical tradeoffs in organismal design	Distinct species occupy the margin of a fitness peak in a community	Functionally distinct species are at a margin of phenotypic space and are steadily present in the community over time
Species interactions (Case 4)	Resource competition theory; mutualisms; consumer-resource dynamics; ecosystem engineers	Interactions alter the local fitness landscape and generate functionally isolated regions	Species are functionally distinct in the presence of interacting species and non-distinct in their absence

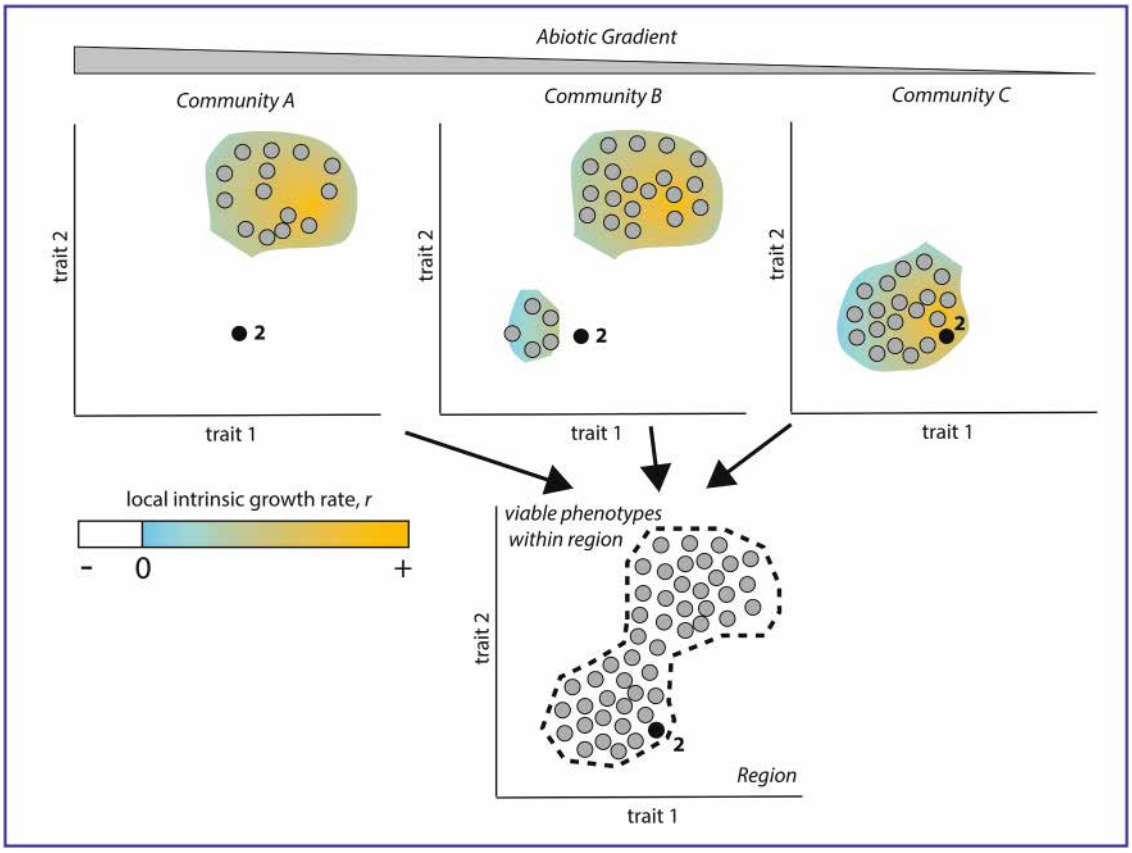

FIGURE 2 Spatial variation in the abiotic environment within a region is expected to produce variation in the intrinsic fitness landscape across local communities. The union of these local fitness landscapes can be used to define the possible phenotypic space within a region (bottom). Comparing fitness landscapes across communities within an area can reveal spatial source-sink dynamics, showing how species 2 becomes functionally distinct in communities A and B by dispersing from community C.

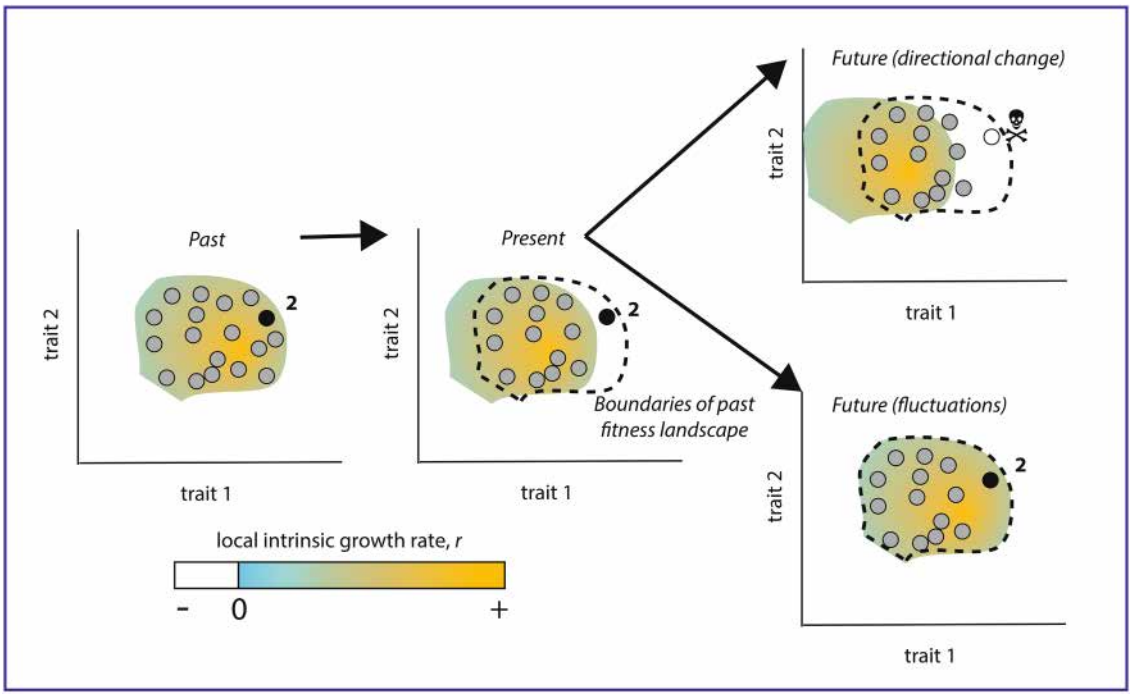

FIGURE 3 A temporal variation in the abiotic environment entails variation in the fitness landscape between past, present and future. Species that persist in the new abiotic environment without traits adapted to it may become functionally distinct, as shown for species 2 in the present (Case 2B). Species 2 will go locally extinct because its phenotype is not adapted to present nor the future abiotic environment in the case of directional changes but can persist in the community for some time before getting extinct (right-top) or be again well adapted under future conditions under environmental fluctuation (right-bottom).

locality can lead to the success of distinct phenotypes (Kraft & Ackerly, 2014). Third, the distinct peaks can represent alternative phenotypic solutions to challenges posed by a uniform abiotic environment (Marks & Lechowicz, 2006). For example, warm desert ecosystems are often home to vegetation that varies widely in drought strategies ranging from annual herbaceous, woody, drought-deciduous and evergreen plants (Dimmitt, 2000). These different strategies may be viewed as distinct alternative designs that can all yield positive intrinsic population growth rates. For instance, in freshwater fish assemblages, distinct functional groups can coexist with alternative resource-use strategies (Brind'Amour et al., 2011). In microbial communities, bacteria with alternative metabolic pathways can coexist (Daims et al., 2015).

Regardless of the source of multimodality (multimodal resource spectra, patchy environments or alternative designs), the peaks in the landscape may differ in importance and species richness. The phenomenon can allow the emergence and persistence of functionally more distinct species within the community when few species occupy an eccentric peak in the fitness landscape (Figure 1c, see species 1 to illustrate case 1).

Case 2: Sink populations

There are many cases of populations with negative intrinsic growth rates, which are typically described as 'sink' populations (Pulliam, 2000) (Figure 1c, see species 2 to illustrate case 2). Both temporal and spatial variations in environmental conditions may cause a species to occur as a sink population in a local community (Chesson, 2000; Levins, 1968). Such sink populations have trait combinations that do not allow positive growth in the local environmental conditions. These trait values can depart from one or several fitness peaks including the 'core' species that are well adapted, and then be functionally distinct (Figure 2) (Enquist et al., 2015; Johansson et al., 2011; Olden et al., 2006; Saar et al., 2012; Supp et al., 2015).

Case 2A: Spatial sink populations

The simplest case of a spatial sink population emerges when species disperse from a locality where they have a positive intrinsic growth rate (the 'source'; Figure 2 Community C) to a locality where their growth is negative (the 'sink'; Figure 2 Communities A and B). Negative growth in the sink locations arises because of a mismatch between species traits and local environmental conditions (Gibson et al., 1999; Grime, 1998; Keddy, 1992; Kraft, Adler, et al., 2015). A species can be consistently part of the community, even with a negative growth rate, if there is regular immigration of individuals from some source populations (Koffel et al., 2022; Mouquet & Loreau, 2003). Spatial sink populations have been a topic of study for decades in ecology. For instance, up to 30%

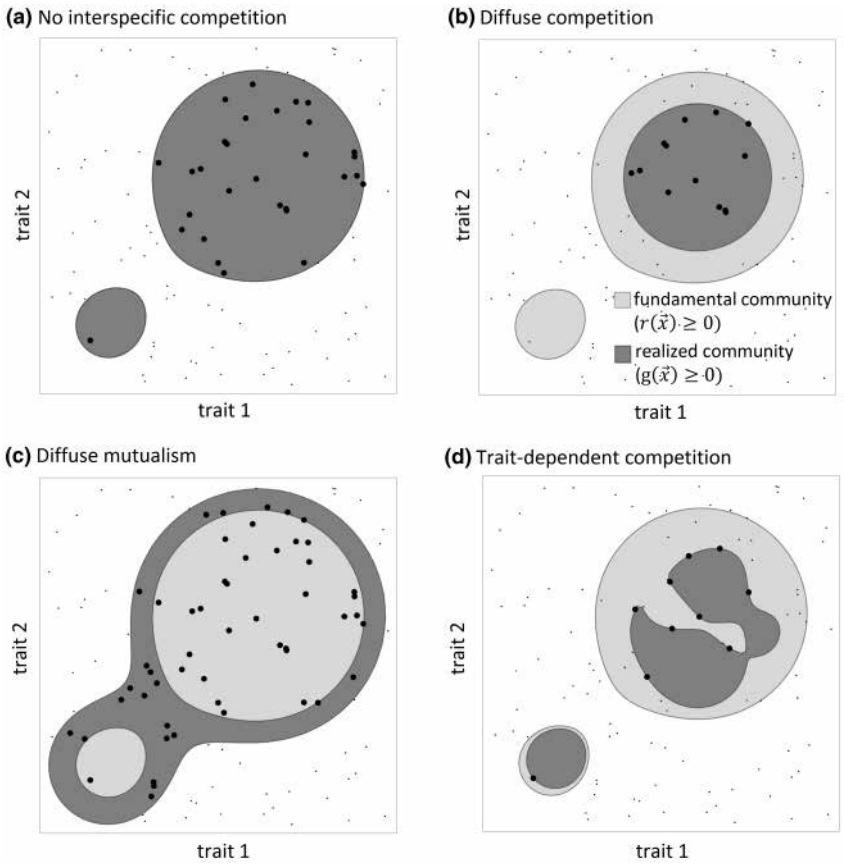

FIGURE 4 The effect of interspecific interactions on the realized community (trait-space with positive fitness $g(\vec{x}) \geq 0$). Coexisting species are indicated by large dots, extinct species by small dots. (a) The case of no species interactions, analogous to Figures 1–3. All species with positive intrinsic fitness can coexist. (b) Diffuse competition ($\alpha_{\text{inter}} = 0.1$) reduces the range of coexisting trait combinations while (c) diffuse mutualism ($\alpha_{\text{inter}} = -0.01$) increases it to include species outside the fundamental community. (d) Trait-dependent competition, modelled by a Gaussian competition kernel with $\sigma = 0.35$ leads to more over-dispersed traits.

of the species in Judean Desert Plant communities are maintained by immigration from adjacent communities (Shmida & Wilson, 1985), and both birds (Veit, 2000) and fishes (Magurran & Henderson, 2003; Pont et al., 2018) are known to migrate to habitats outside their fundamental niche.

A full understanding of this mechanism would require comparing local fitness landscapes across nearby localities (Figure 2) and assessing species dispersal capacity. Alternatively, from a metacommunity perspective, it is possible to assess the spatial connectivity of communities and the temporal stability of populations to identify core and satellite populations (Collins & Glenn, 1991).

Case 2B: Temporal sink populations

Changing environmental conditions can lead to circumstances where species that were well adapted are still present in a community despite having negative intrinsic growth rates under current conditions (extinction debt, Tilman et al., 1994). This can occur either due to directional change in climate over time (e.g. bristlecone pines, Kroiss & HilleRisLambers, 2015) or temporal fluctuations (e.g. interannual variation, Angert et al., 2009). Species having trait values that were adapted to past conditions are expected to be functionally distinct in a current adaptive space with shifted fitness peaks (Figure 3). For example, cold-adapted diatoms from Lake Baikal that bloom under ice have distinct thermal traits with lower temperature optima than other species. They were widespread in the past but are now endemic to Lake Baikal and are declining in abundance due to decreasing ice cover (Wollrab et al., 2021). Similarly, paleoecological studies suggest that trait composition has changed during past climate change events (Gaüzère et al., 2020; Ordonez & Svenning, 2015, 2016). Temporal environmental variability (rather than directional change) can also produce shifting fitness peaks over time. Such variation can allow the persistence of functionally distinct although less adapted species at a given time, a phenomenon also called 'storage effect' (Chesson, 2000). For example, interannual variation in the timing of rainfall in the Sonoran Desert can favour the coexistence of annual plants with contrasting functional traits (Angert et al., 2009).

Although several frameworks can be used to identify remnant or sink species in communities (Cadotte

BOX 1 Variation in functional distinctiveness independent from the fitness landscape

The causes of functional distinctiveness detailed in cases 1 to 4 arise through deterministic trait-dependent population dynamics. However, stochastic dynamics can modulate the observed patterns of distinctiveness in a community. For example, dispersal limitation, spatial constraints on the packing of individuals and other related sampling effects can prevent occupancy of fitness landscape despite positive intrinsic growth rates. In case of purely neutral assembly, local community members can be viewed as a random sample of a larger species pool of viable community members. Such random sampling can create local communities with functionally distinct members by chance alone, despite the locally distinct species being functionally indistinct in the larger species pool. To illustrate this situation, we simulated local communities of varying sizes, with members sampled from a static species pool. Small sample sizes produced substantially more variability in the average distinctiveness values of resident members relative to the regional average distinctiveness (Figure 5). This means that small assemblages can include functionally distinct species simply by chance. Such stochastic variation in functional distinctiveness should be quantified and used to formally test whether observed distinctiveness patterns deviate from a dispersal or sampling-based null model.

In addition, because of the stochastic extinction and colonization dynamics, we expect that many communities will have regions of the intrinsic fitness landscape that are unoccupied at certain points in time. This can allow, for instance, functionally distinct nonnative species to invade the community (cf. Naturalization Hypothesis, Darwin, 1859).

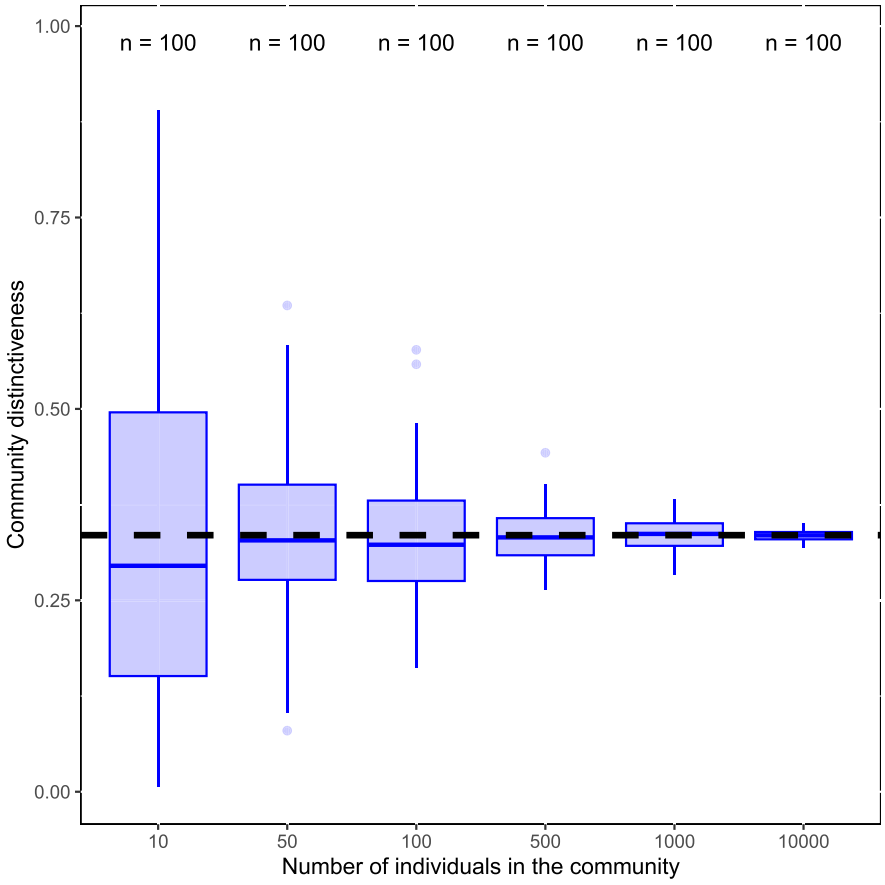

FIGURE 5 Average distinctiveness in neutral communities as a function of community size, where communities are at a migration-drift equilibrium. The dashed horizontal line is the distinctiveness in the regional pool providing immigrants. For smaller size, sampling effect entails a wide variation of the average distinctiveness in communities. We performed the simulations using the *coalesc* function in *ecolottery* R package (Munoz et al., 2018), with migration rate $m = 0.05$. n is the number of simulations making the boxplot for each community size.

& Lovett-Doust, 2007; Magurran & Henderson, 2003; Umaña et al., 2017), a formal empirical evaluation of the link between temporal sink population and their functional distinctiveness has still to emerge. The connection between the transient nature of sink populations and their functional distinctiveness is particularly challenging to assess because it implies characterizing the past species composition and trait-environment relationship of the community. Fossil data, seed bank studies, or long-time series observations may be useful in this respect (e.g. Harrison et al., 2010).

Case 3: Species at the margin of the fitness landscape

Let us consider a fitness landscape including a major peak in which most of the well-adapted species are located, while some species at the margin of the peak have a lower but still positive population growth. The later species can be functionally distinct and still be maintained in the community (Figure 1c case 3). An instance of such case is when boundaries of the functional space express biophysical constraints (Niklas, 2007; Rothstein & Zak, 2001), developmental constraints (Gould et al., 1979) and/or the ecological costs of suboptimal design (Onoda et al., 2014). For example, metabolic scaling theory suggests limits to body size at both upper and lower bounds, representing viability limits and a marginal position on the fitness landscape (Enquist et al., 2009; Niklas, 2007). Similarly, because height in trees is limited by water transport biophysics, *Sequoiadendron* is located at the edge of plant phenotypic space and is functionally distinct (Díaz et al., 2016; Koch et al., 2004).

Another possible situation is when directional selection is playing and modifying the fitness landscape towards positive values in some novel areas of the functional space. Distinct species can be located at the leading edge of migrating viable space during the process, which represents a margin of the fitness landscape at this time. Furthermore, irrespective of the existence of biophysical constraints and directional selection, some species can be functionally distinct simply because they are located at the edge of the fitness landscape, as a kind of 'edge effect'. In any case, note that we posit here that fewer species might be located at a marginal position in phenotypic space, that is, in a tail of functional trait distribution, but these species might be still locally abundant.

Case 4: Species interactions

In cases 1–3 above, we have focused on the relationship between the focal species and its abiotic environment encoded in the intrinsic fitness function $r(\vec{x})$. In this perspective, species interactions do not change the landscape (Figure 4a). However, ecology has historically mainly focused on exploring the myriad ways species may impact one another and affect their relative performance (Vellend, 2016). Within our framework, we can consider how a second species may alter the intrinsic fitness landscape, by raising or reducing the height of fitness peaks and deepening valleys between them, creating new viable areas in the fitness landscape and, in general, creating more complexity in the realized fitness landscape (Figure 4b–d).

In our Lotka-Volterra model (1), the realized fitness landscape is given by $g(\vec{x}_i) = r(\vec{x_i}) - \sum_{j=1}^{N} \alpha(\vec{x_i}, \vec{x}_j) N_j$. First, in the simplest case of diffuse interactions, where each species affects each other equally ($\alpha(\vec{x}_i, \vec{x}_j) = \alpha_{\text{inter}}$ constant and independent from species traits), the realized community is simply contracted by negative interaction (Figure 4b) and expanded by positive interactions (mutualism, Bulleri et al., 2016) (Figure 4c). Second, when trait-based competitive interactions favour species with more dissimilar traits (limiting similarity), the exclusion of species neighbouring in fitness landscape increases functional evenness and the functional distinctiveness of persisting species (Figure 4d) (Dayan & Simberloff, 2005; Ranjan & Klausmeier, 2022). Third, interactions can modify specific areas of the landscape by either enhancing or decreasing population growth rates there. For instance, ecosystem engineers can modify the local abiotic conditions and enlarge the regions of intrinsic landscape with positive fitness, and thus allow novel and distinct trait combinations to establish (e.g. cushion plants sheltering subordinate plant assemblages, Raevel et al., 2018). Conversely, direct negative interactions by consumers can create functional distinctiveness among their resource species. A voracious consumer, or the combined effects of multiple consumers, can lead to the depletion and even extinction of resource species in the range of trait values appealing to the consumer species (Abrams et al., 2008). In many other cases, though, the negative interactions can be indirect. For instance, they can be mediated by introducing a parasite by non-native fishes, which decreases the fitness of native fishes (Gozlan et al., 2005).

Empirical tests of the influence of interactions on functional distinctiveness can involve comparing species performance in communities with and without the presence of interactors (e.g. by measuring a Relative Neighbour Effect to assess facilitation, Callaway et al., 2002).

DISCUSSION

Recent research has emphasized the important role that functionally distinct species can play in communities, with implications for community structure, ecosystem functioning and biodiversity conservation (Brun et al., 2022; Delalandre et al., 2022; Grenié et al., 2018;

Loiseau et al., 2020). However, functional distinctiveness can arise in communities for a diversity of reasons. We argue that it is critical to understand the causes of functional distinctiveness and that not all causes of functional distinctiveness matter equally. To drive research on this topic forward, we develop a fitness landscape framework where species' intrinsic growth rates depend on the interaction of their traits with local abiotic conditions (Cases 1–3) and with biotic interactions (Case 4).

Considering the causes of functional distinctiveness in ecology and conservation

While it may be tempting to assume functionally distinct species play similar roles in their respective communities or ecosystems, we argue that the contribution of functionally distinct species to community dynamics, ecosystem functioning and future conservation value depends intimately on the mechanisms that have led them to be functionally distinct. For example, a species that is functionally distinct due to directional climate change that has reshaped the fitness landscape (Case 2B, Figure 3) or because of spatial source/sink dynamics (Case 2A, Figure 2) may make unique contributions to current ecosystem functioning (e.g. Fryxell, 2001; Mouquet & Loreau, 2003; Verspoor et al., 2008) but be selected against in future conditions. Conversely, a species that is distinct because it occurs at the margin of a fitness landscape (Case 3, Figure 1c) or because it is located on an isolated fitness peak (Case 1) may offer critical insurance for future ecosystem functioning (Violle et al., 2017), especially if ongoing environmental changes alter the local fitness landscape in favour of the distinct phenotypes. However, in cases where the fitness landscape depends on species interactions (Case 4), removing one species can have counterintuitive or surprising impacts on community structure and functioning. A growing body of research addresses how to connect trait differences to the outcomes of species interactions, which should help characterize the emergence and persistence of functionally more distinct species in this case (e.g. Fortunel et al., 2016; Kraft, Godoy, & Levine, 2015; Kunstler et al., 2016; Litchman & Klausmeier, 2008).

Connecting the fitness landscape to community and ecosystem dynamics

The trait-based ecology enterprise rests on the understanding that species trait variation can inform differences in demographic performance (Coulson et al., 2006; Salguero-Gómez et al., 2018; Violle et al., 2007). However, our understanding of the functional basis of variation in fitness is currently incomplete for most, if not all, taxa (but see Adler et al., 2014; Kandlikar et al., 2022; Litchman & Klausmeier, 2008; Wright et al., 2010; Yang et al., 2018). Resolving the phenomena explored in this paper will require a better understanding of the fitness landscape (Figure 1) for many groups, and the approaches for doing so are now well-established (e.g. Klausmeier et al., 2020; Laughlin et al., 2020).

It is widely understood in functional ecology that not all traits matter equally for all ecological processes of interest (Diaz & Cabido, 2001; Kraft, Godoy, & Levine, 2015). For example, traits that govern species' demographic responses to abiotic conditions ('response traits', Figure 1) might not always be the same traits that dictate the effect that species have on ecosystem processes ('effect traits'). In groups where response and effect traits are distinct, it will be essential to understand the link between the functional distinctiveness of response and effect traits to disentangle the cause and consequences of distinctiveness in the community. Our framework can be applied directly in the simplest cases where response and effect traits are the same or where functional distinctiveness in response and effect traits are perfectly correlated. Conversely, response and effect traits may be unrelated (Lavorel & Garnier, 2002), so that a species with indistinct response trait values located on a central peak of the local fitness landscape may exhibit functionally distinct effect trait values. Further progress in this area will require research into the correlation structure in the distinctiveness of responses vs. effect traits within clades.

In order to make our framework applicable, one would need to be confident enough in the trait-performance landscape that had been measured and in the nature of functional dimensions related to abiotic and biotic determinants. This implies addressing a number of critical issues at the core of the research agenda in functional ecology. In particular, it requires overcoming the difficulty of measuring the functional distance between species using multiple traits, for example, when the traits are in different units or log-transformed, categorical and considering the effects of trait–trait covariation on functional distances (Grenié et al., 2017; Mouillot et al., 2021).

The scale dependence of functional distinctiveness

Thus far, we have focused on the ecological causes of functional distinctiveness within local communities. However, given the role that regional species pools play in shaping patterns of functional distinctiveness (e.g. Case 2) as well as the role that constituent local communities play in forming the species pool, it is also important to consider how patterns of functional distinctiveness depend on a spatial scale (Grenié et al., 2018; Mouillot et al., 2021; Gaüzère et al., 2023). For example, suppose a species is specialized to a rare habitat. In that case, it can

be functionally indistinct in this habitat but functionally distinct when compared to species of other habitats in a regional pool. It is also possible for species to be functionally distinct at all spatial scales if they are located at a margin of a fitness landscape (Case 3) globally (e.g. sharks in marine megafauna, Pimiento et al., 2020). We also expect some of the mechanisms we have highlighted to produce spatial variation in functional distinctiveness to change over time, including source-sink (Case 2) and neutral (Box 1, Figure 5) dynamics. This suggests that more work is needed on the patterns and causes of variation in functional distinctiveness at larger spatiotemporal scales.

Connections to evolutionary dynamics

While we have focused here on ecological drivers of local patterns in functional distinctiveness, the functional composition of communities and species pools ultimately reflects the legacy of evolutionary dynamics and speciation events over the long run (Vellend, 2016). For example, the evolution of key innovations can generate functionally distinct lineages initially, though distinctiveness may decline over time if evolutionary radiation makes the innovation more common or if different lineages converge towards similar phenotypes (Deline et al., 2018; Miller & Stroud, 2022). Although a full discussion about the evolution of distinctiveness is beyond the scope of this paper, future research should explore the connections between ecological and evolutionary drivers of functional distinctiveness in communities. For example, it is still uncertain whether functional distinctiveness is related to phylogenetic distinctiveness. Several studies have suggested a weak, if any, relationship (Cornwell et al., 2014; Grenié et al., 2018; Jetz et al., 2014). Contrasting relationships are expected depending on underlying evolutionary and biogeographic processes. A positive correlation should be found in the case of functional paleoendemic species adapted to a different historical climate (e.g. Southern hemisphere coniferes, Rundel, 2019). Such a positive correlation implies that the functionally distinct traits are associated with low diversification or evolutionary dead ends. Conversely, a negative correlation occurs with strong niche conservatism and rapid divergence in a young lineage. The absence of correlation (Liow, 2007) occurs when recent evolutionary radiations break a relationship between phylogenetic and functional distinctiveness. To better understand the linkage between functional and phylogenetic distinctiveness, further studies of the emergence and linkage at the intraspecific level are needed (Vasseur et al., 2018). In this perspective, our framework also provides a way to address the emergence and maintenance of genotypes bearing original phenotypes within species.

Embracing the multiple facets of rarity

Functional distinctiveness is one of the facets of ecological rarity. Other facets include functional uniqueness, the distance to a nearest neighbour in functional space and other taxonomic components based on local species abundance and regional frequency (Violle et al., 2017). We considered here the case of functional distinctiveness as a relevant indicator of the influence of a rugged fitness landscape on community dynamics and composition. We acknowledge that the fitness landscape perspective further offers a relevant basis for investigating the drivers of other facets of rarity in future works.

We considered here a metric of functional distinctiveness based on species occurrences, but it can also be weighted by species abundances (Violle et al., 2017). Our framework addresses the emergence and persistence of more distinct phenotypes irrespective of their abundance. We did so because we based our reasoning on the concept of intrinsic fitness that relates to the ability of species to increase when rare and not to their equilibrium abundance. Nevertheless, a relevant perspective would be to address whether and how species with distinct phenotypes become abundant in a community. For this purpose, the Lotka-Volterra model (Equation 1) offers a way to model and analyse abundance dynamics under the dependence of functional traits.

CONCLUSIONS

Our conceptual framework provides a novel perspective on how heterogeneous fitness landscapes may cause the emergence and persistence of functionally more distinct species in communities, a perspective that is missing in traditional views of communities that emphasize community-weighted trait means and unimodal trait-performance relationships. We make predictions and offer examples for four possible hypotheses for functional distinctiveness. This work can advance trait-based ecology and our understanding of functional distinctiveness by providing a framework and means to distinguish among them. Future research should prioritize a more detailed understanding of trait-performance relationships. A further avenue would be to characterize and relate the influence of ecological and evolutionary processes on local and regional distinctiveness, respectively, to develop a multiscale perspective on functional distinctiveness. Phenotypic diversity, especially related to functional distinctiveness, connects directly to the ecophysiological mechanisms that drive population and community dynamics and, therefore, should be a central aim of understanding and conserving biodiversity.

AUTHOR CONTRIBUTIONS

Designed study: Nathan J. B. Kraft; led writing: François Munoz and Nathan J. B. Kraft; performed simulations: François Munoz and Christopher A. Klausmeier; visualizations: Nathan J. B. Kraft, François Munoz and Christopher A. Klausmeier; secured funding: Cyrille Violle; all authors contributed to conceptual discussions, writing and revisions.

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No new data has been used for this work.

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