

A functional approach reveals community responses to disturbances

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Understanding the processes shaping biological communities under multiple disturbances is a core challenge in ecology and conservation science. Traditionally, ecologists have explored linkages between the severity and type of disturbance and the taxonomic structure of communities. Recent advances in the application of species traits, to assess the functional structure of communities, have provided an alternative approach that responds rapidly and consistently across taxa and ecosystems to multiple disturbances. Importantly, **trait-based metrics may provide advanced warning of disturbance to ecosystems because they do not need species loss to be reactive.** Here, we synthesize empirical evidence and present a theoretical framework, based on species positions in a functional space, as a tool to reveal the complex nature of change in disturbed ecosystems.

Disturbance and biodiversity: why traits should matter
Despite conservation efforts, biodiversity loss continues apace at regional or global scales across a wide range of ecosystems, due to increasing intensity of disturbances (see [Glossary](#)), such as overexploitation of species [1], destruction of habitats [2], climate change [3], or invasion by alien species [4]. As a feedback, biodiversity erosion is imperiling the sustainability of ecological processes and the provision of ecosystem services [5]. Thus, there is an urgent need to quantify and predict the effects of disturbance on biodiversity patterns to guide conservation efforts and the management of ecological resources. Here, we consider the term ‘disturbance’ in its widest sense as any event, natural or human-driven, that causes temporary and localized shifts in species demographic rates. We classify disturbances in three categories as those caused by (i) direct human impacts; (ii) biotic pressure (mainly imposed by exotic species); and (iii) environmental changes (abrupt shifts in abiotic conditions and habitat degradation).

Until recently, the effect of disturbance on species diversity was largely assumed to be unimodal, with species diversity reaching its maximum at intermediate levels of disturbance [6]. The underlying mechanistic explanation

for this pattern is that competitive exclusion may reduce species richness at low levels of disturbance, whereas high levels of disturbance exclude all but the most disturbance-tolerant species. However, the unimodal model is far from universal, having been falsified by observational [7], experimental [8], and theoretical studies [9]. Moreover,

Glossary

Disturbance: any event, natural or human driven, that causes temporary and localized shifts in demographic rates.

Fourth-corner analysis: a method that quantifies the correlations between species traits and abiotic variables in a fourth matrix using three input matrices (R, abiotic variables; L, species presences and/or absences or abundances; and Q, species traits).

Functional dissimilarity: the dissimilarity in the functional space occupied by two communities.

Functional divergence: the proportion of total abundance supported by species with the most extreme trait values within a community.

Functional diversity: the distribution of species and their abundances in the functional space of a given community.

Functional evenness: the regularity of the distribution and relative abundance of species in functional space for a given community.

Functional identity: the mean value of functional traits, weighted by abundance, across all species present in a given community.

Functional originality: the isolation of a species in the functional space occupied by a given community.

Functional richness: the volume of multidimensional space occupied by all species in a community within functional space.

Functional space: a multidimensional space where the axes are functional traits along which species are placed according to their functional trait values.

Functional specialization: the mean distance of a species from the rest of the species pool in functional space.

Functional trait: any trait directly influencing organismal performance.

Linear trait-environment method (LTE): a method that linearly relates species traits to abiotic variables using species abundances across environments.

Maximum Entropy model (MaxEnt): a predictive model assuming that the relative abundance of a given species in a given environment is a function of its trait values.

Monotonic relation: a relation is monotonic if a response or dependent variable consistently increases (or decreases) or stays the same with every increase in an associated predictive or independent variable.

Performance filter: the process by which local abiotic variables determine the performance of a given trait, defined as its fitness, in a given environment.

RLQ analysis: a three-table (R, abiotic variables; L, species abundances; Q, species traits) ordination method testing the relations between species traits and abiotic variables.

Trait filtering: the process by which abiotic variables determine whether a species has the requisite traits to colonize, establish, and persist in a given environment.

Trait: any morphological, physiological, or phenological feature usually measurable at the individual level.

Unimodal relation: a relation is unimodal if a response or dependent variable has a single mode (or peak) along the axis of the predictive or independent variable.

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Review

neutral models [10], where all species are ecologically identical [11], also produce unimodal relations between species richness and disturbance level. This challenges the assumption that the unimodal model is due solely to species differences in terms of tolerance to disturbance or competitive ability. It also indicates that species diversity alone cannot explain whether niche or neutral processes are responsible for the observed patterns.

Functional traits offer a useful alternative approach, providing a means of distinguishing between niche and neutral assembly processes [12–14]. Indeed, accumulating evidence suggests that competitive interactions [15] and species filtering by disturbance [16] are, at least partly, driven by species functional traits. Disturbance generally increases mortality rates and reduces reproduction rates for resident species, causing density-dependent competition to have a weaker influence on community structure (but see [17]). Usually, some species are more severely impacted by disturbance than others, but this can occur with both niche and neutral models. When disturbance excludes species with particular traits, or severely reduces

their abundance, trait differences between species can drive interspecific differences in response to disturbance [18]. This provides evidence for niche processes driving community responses to disturbance and permits falsification of the null hypothesis (that species are identical in their response to disturbance) provided by neutral theory (Figure 1). Rejection of the neutral model for response to disturbance allows prediction of disturbance impacts on the functional trait structure and, hence, the functioning of communities [19]. However, the use of traits to reject the neutral model requires metrics that can detect disturbance impacts on the functional structure of communities. To understand which metrics might be useful for detecting non-neutral disturbance impacts on functional structure, it is helpful to envisage species trait values as coordinates locating species in functional trait space. Here, we define functional space as a multidimensional Euclidean space where axes are ecologically relevant traits (Box 1). Thus, where species diversity, as a sole metric, cannot reliably distinguish between selective (niche) and random (neutral) processes in shaping the response of communities to disturbance [9,10], we propose that a trait-based approach can better quantify, and so predict and anticipate, the impacts of disturbance on ecological communities. In scenarios where both theories apply, species traits provide the means

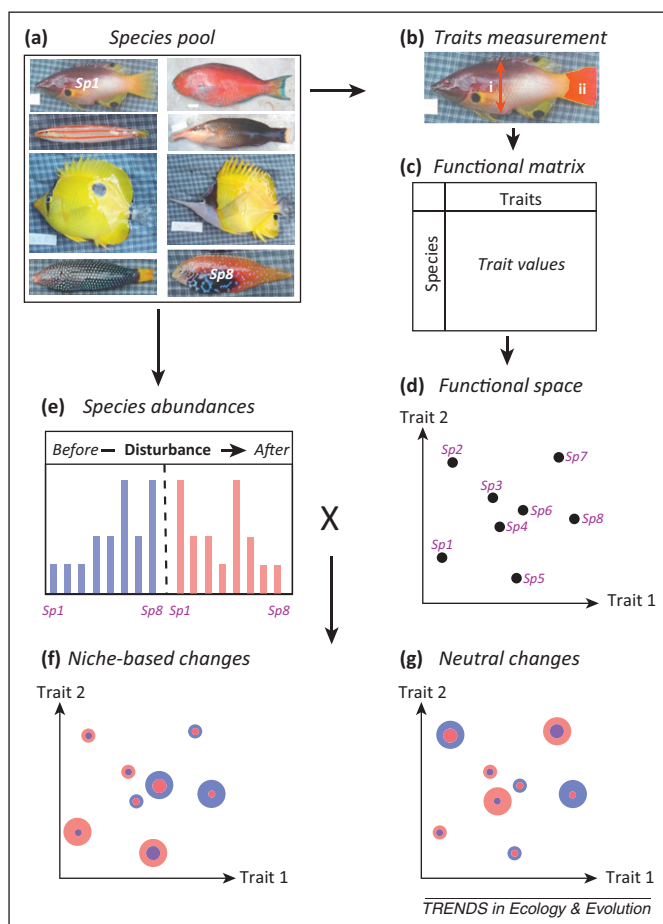


Figure 1. Impact of disturbance on the functional structure of a theoretical species assemblage. (a) Eight species comprising the pool (from Sp1 to Sp8). (b) Examples of functional traits measured on individuals: (i) body depth; and (ii) caudal fin surface. (c) Mean trait values calculated for each species. (d) Species plotted in a functional space where axes are mean trait values. (e) Species abundances before and after disturbance. (f) Under the niche hypothesis, loser species [i.e., those with lower abundance after disturbance (proportional to pink circle surface) than before (proportional to blue circle surface)] share common trait values. The winner species are also functionally similar to each other, but are different from loser species. (g) Under the neutral hypothesis, loser and winner species are randomly placed in the functional space.

Box 1. History, definition, and use of functional space

It has long been accepted that the morphology of a species can be a reliable indicator of its ecology [88–90]. However, it was the widespread use of ordination methods that provided a readily accessible methodology to express these relations [91]. Ordinations permitted the simultaneous examination of multiple traits in multiple organisms. One can visualize entire communities or assemblages in terms of the functional abilities of both the assemblage as a whole and the component species [33,59,92]. Thus, complex anatomical structures could be quantitatively compared and variation interpreted in an ecological context. With this association between form and function, a description of functional morphospace was possible as a multidimensional measure of the abilities of organisms.

If non-anatomical traits are included (e.g., biochemical and behavioral traits), the potential information is even greater [51]. The use of morphospace, trait space, or functional morphospace has steadily evolved over the past few decades. All can be easily contained in the single term, functional space; that is, the ecological attributes of species (occurrences or abundances and traits) or assemblages expressed in multidimensional space.

Although popular in paleontological studies, where morphology provides insights into past ecology [23,93], it is in neontology that it has been most widely used. From birds [21], bats [94], and fishes [88] to insects [95] and plants [59], the approach has provided key insights into the functional structure of assemblages. However, mirroring the relation between species diversity and functional diversity [96], the devil is in the detail. From the start, the ecological links were made with caution [92] and links may not always be as strong as one may assume [88,91,97]. Thus, although functional space remains a powerful tool, the strength of the application depends on the extent to which traits really are indicative of functional attributes.

Nevertheless, the evaluation of functional space has proven to be an exceptionally versatile and sensitive approach, offering insights into the changes in assemblages through time [13,23], the impacts of species invasions [32,33], and responses to environmental change [16,42]. This single approach offers a rigorous and powerful methodology to identify and distinguish the functional implications of changes in assemblages.

to determine the relative magnitude of niche versus neutral processes in disturbed communities [20]. Moreover, measures of the functional traits within a community are better predictors of ecosystem processes than is species diversity [21]. Thus, quantifying and predicting functional community structure within a context of increasing disturbance intensity and frequency is required to anticipate the potential loss of ecosystem services that is indisputably associated with biodiversity erosion [5].

Here, we first propose theoretical expectations regarding the influence of three common types of disturbance (i.e., direct human impacts, biotic pressures, and environmental changes) on the functional structure of communities. **The functional structure of a community is defined as the distribution of species and their abundances in the functional space.** We compare expected trends of taxonomic versus trait-based indices of community structure along disturbance gradients to argue that trait-based indices are more likely to show monotonic and predictable relations. We also present empirical evidence supporting this theoretical view. We then review a list of complementary quantitative tools that can be used to assess changes in functional community structure under disturbance, as well as appropriate null models and recent methods to

test them. We show why and how a trait-based multidimensional framework may provide advanced signals of disturbance on ecosystems. Finally, we discuss future directions and knowledge gaps regarding this rapidly evolving research field.

Impacts of disturbance on functional community structure: empirical evidence

The use of multidimensional functional space based on species traits (Box 1, Figure 1) is emerging as a particularly useful way to characterize changes in communities or to test various ecological theories [19,22,23]. Here, we use functional space to illustrate and quantify expected changes in community structure after disturbance under the niche hypothesis (i.e., that traits matter). We partition disturbances to ecological communities as direct human impacts, biotic pressure, and environmental changes (Figure 2).

Direct human impacts

We restricted human impacts to those that directly affect species composition and abundances, mainly through resource exploitation. The total trait space occupied by a community declines in a non-random way according to the

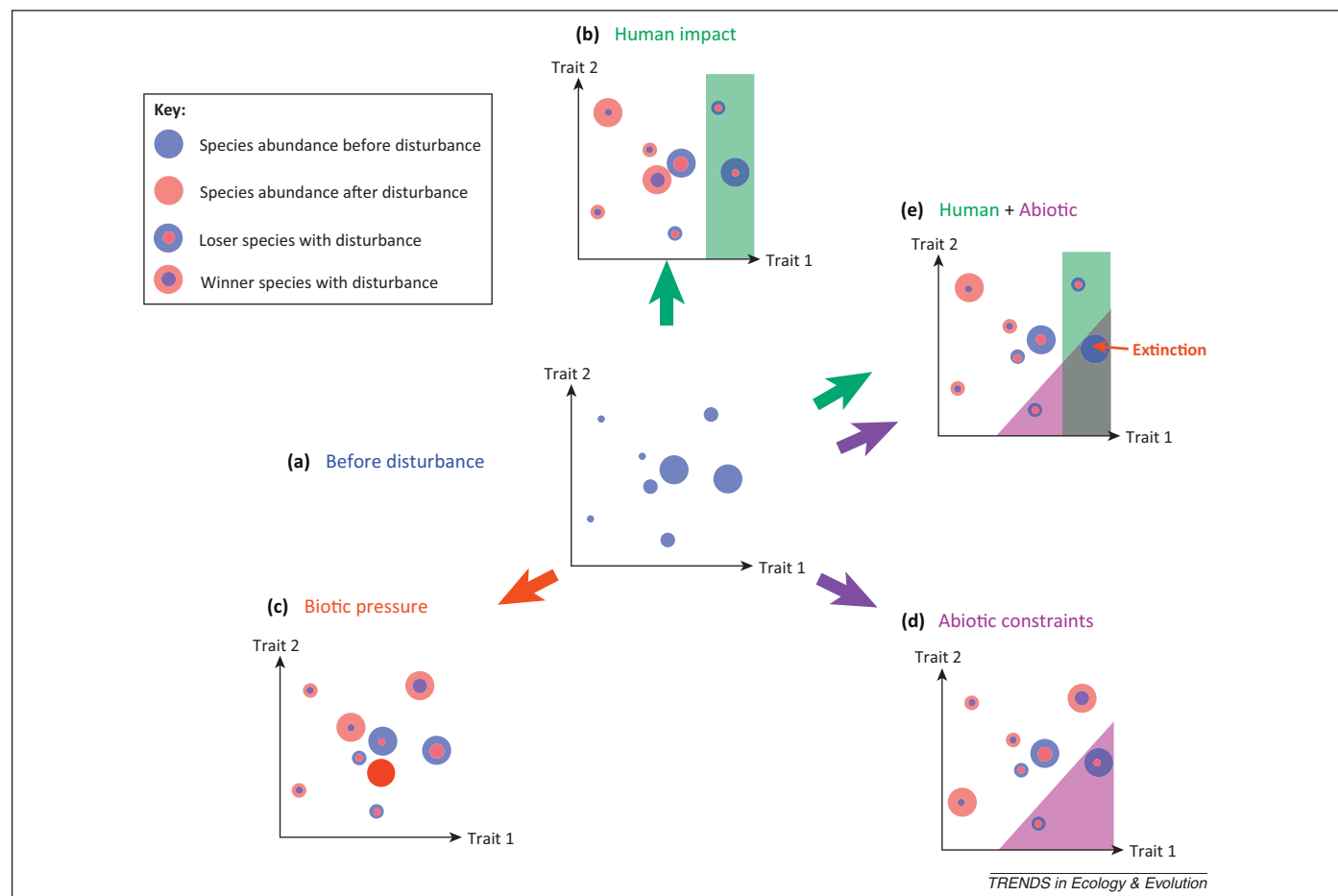


Figure 2. Theoretical changes in the functional structure of a species community after three types of disturbance. (a) Functional space defined by two traits where eight species are included. (b) Human impact depletes species populations with high values for trait 1. (c) Biotic pressure, through the presence of a non-native species (solid red circle), depletes the population either of the closest native species in the functional space by competition or of the most vulnerable species to predation. (d) Environmental constraints filter out species with high values for trait 1 and low values for trait 2. As an illustration, one combination of pairs of disturbances (e) is also presented, with some additive impacts in the functional space inducing the extinction of a species.

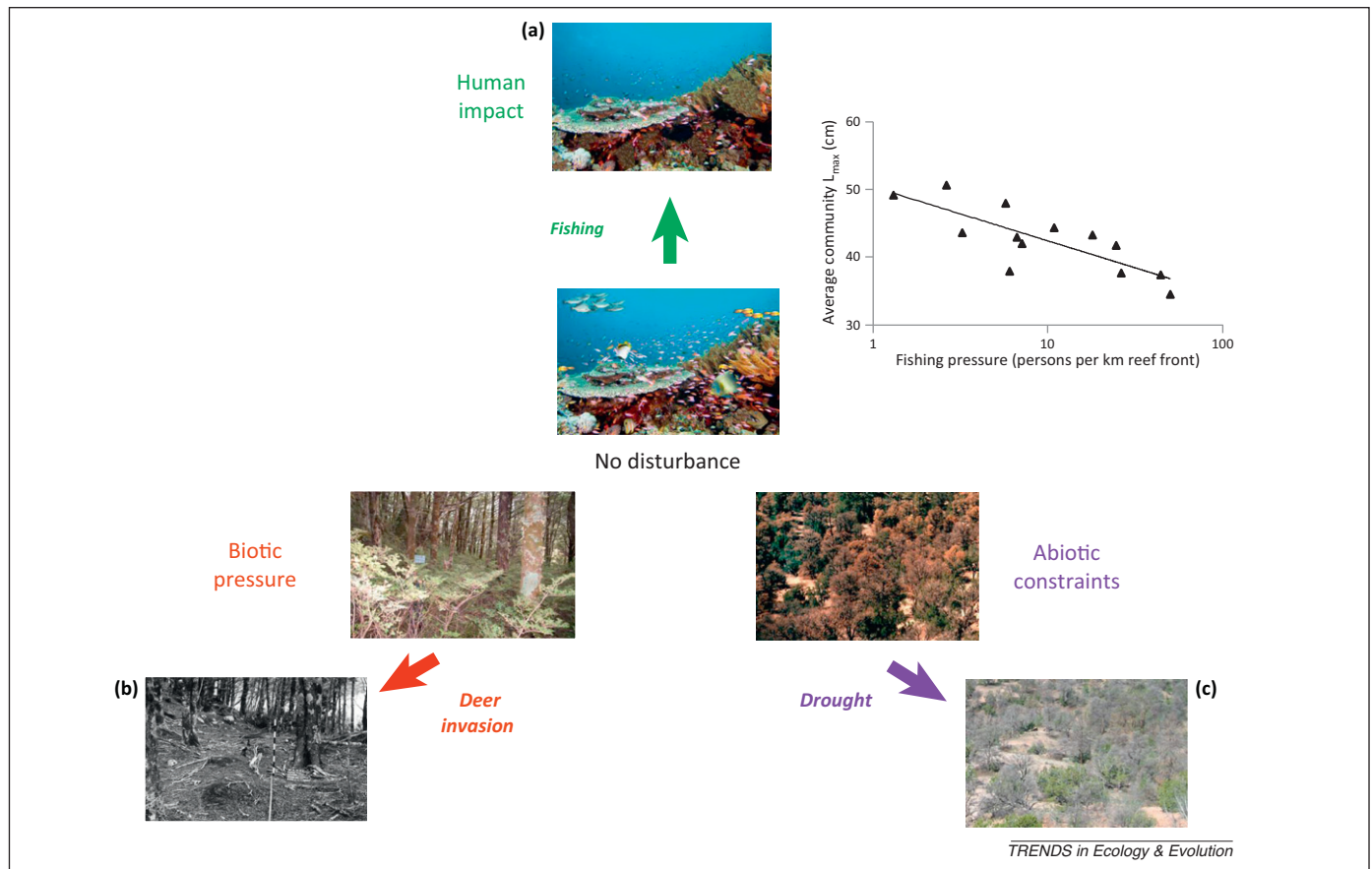


Figure 3. Illustration of the impact of three types of disturbance on functional community structure. (a) Impact of fishing on coral reefs where large-bodied species are preferentially targeted. Results from the Lau Island group (Fiji) show that fishing pressure explains 63.6% of variation in the weighted average maximum size of the fish community [98]. (b) *Nothofagus* forest in New Zealand before (1970s) and after control of invasive deer, which impact palatable species with high foliar nutrient contents (nitrogen and phosphorous). (c) Drought impact on the forest around Los Alamos (Arizona, USA) before and after drought stress mostly affecting tall, overstory trees as well as shorter trees, shrubs, grasses, and other vegetation beneath the overstory trees.

niche theory because human impact preferentially affects species sharing some vulnerable traits and, thus, certain parts of the functional space (Figure 2b). The most striking example is the disproportionate loss of large-bodied fishes across the world [24]. Indeed, fish communities are not randomly affected by fishing pressure, with a clear preference for predatory species [25] and species that grow larger [26] (Figure 3a). This profoundly affects community composition and ecosystem functions because even moderate levels of exploitation can drive large-bodied components of major functional groups to local extinction or functional irrelevance. Hence, size-based metrics have proven to be powerful indicators of fish community responses to exploitation [27,28].

As an illustration, the most conspicuous fish species losses on coral reefs are from the most heavily targeted species, such as sharks, groupers, snappers, and larger herbivores [29–31] (Figure 3a). These provide the basis for novel fish communities that are dominated by small planktivorous or herbivorous fishes. Although they are able to deliver many ecosystem services and support food webs, these novel communities represent a fundamentally different species assemblage: a functionally depauperate system created by the selective removal of groups driven by burgeoning human population densities and an increasing trade to western markets driven by gastronomic tastes or desires.

Biotic pressure

Biotic impacts, largely induced by non-native species, may change the local species richness of a given community, as well as its functional structure, by altering a part of the functional space occupied by native species. Typically, the greatest impacts result from changing the composition within the community in a non-random way (Figure 2c), particularly affecting species with similar traits through competition or by species sharing traits, thus making them vulnerable to a consumer. Native and non-native species can be similar in functional traits, but a competitive advantage may allow non-native species to establish and ultimately extirpate native species. For instance, non-native perennial grass invaders can establish into native-dominated grasslands, achieving cover values up to 71% over several years and decreasing native perennial grass productivity [32]. Similarly, the range contraction of native fish species in the Colorado River Basin was partly explained by overlapping traits (morphological, behavioral, physiological, trophic, and life history) with non-native species [33]. These results suggest that non-native species do not need functional traits that are different from those of the native communities to succeed, but may competitively establish and then decrease the abundance of, or even exclude, native species with similar traits. Non-native species can also act as both competitors and consumers to decrease native species abundances until potential

extinction. For instance, the invasion of the ladybird species *Harmonia axyridis* in eastern England provoked the decline of some native aphidophagous ladybirds through competition for prey and intraguild predation of eggs, larvae, and pupae, both of which are linked to trait similarity [34].

As an illustration, the flora of New Zealand has evolved in the absence of ungulate herbivores. The widespread introduction of ungulate herbivores by Europeans has reduced populations of palatable species [35] (Figure 3b). This lowers community-weighted means for foliar nutrient (nitrogen and phosphorous) content and increases them for foliar tannin, phenolic, and lignin content [36]. These trait shifts may also have consequences for rates of litter decomposition and photosynthesis.

Environmental changes

Environmental changes may not only alter total species richness at a location, but can also cause a shift in functional space occupation by removing species with traits that are poorly adapted to the new environment and allowing colonization by better-adapted species (Figure 2d). For example, following long-term changes in precipitation, transitions among grassland and scrubland can occur, causing shifts to woody vegetation and, thus, directional modifications to the functional structure of communities [37]. In the same vein, alpine plants with a longer growing season that are taller (more competitive) with larger leaf areas (more productive) may replace other species in snowpatches because climate change is inducing earlier snowmelt [16]. Also, the relation between fire intensity and species mortality in tropical areas has been closely linked to tree traits, such as diameter, height, and wood density [38]. Hence, fire-induced tree mortality may become predictable from appropriate traits.

Within the context of increased drought intensity and frequency under warmer temperature conditions induced by climate change, forests are experiencing severe die-off events [39]. Spatial patterns of mortality are, however, influenced by species life-history traits, with drought-tolerant species having traits consistent with their mode of stomatal regulation, such as deep rooting access to more reliable soil water and cavitation-resistant xylem [40]. Wood density is a key trait in preventing xylem cavitation [41] and plants with higher density tend to have better resistance in more drought-prone environments [42]. As a result, the juniper woody species *Juniperus monosperma* experienced mortality ranging from 2% to 26% after 15 months of depleted soil water content (2001–2002) in southwestern North America, whereas the overstory tree species *Pinus edulis* (a piñon pine) experienced mortality of up to 90%, inducing potentially large changes in carbon stores and dynamics. This is of concern for carbon-related policies and management (Figure 3c) [39].

Some environmental changes are also directly mediated by humans and impact the functional structure of communities. For example, extinction risk is higher for smaller and more specialized bird species following habitat loss [43], whereas bats with a high wing-tip shape index, making them adapted to flight in complex canopies, are less prevalent in human-altered agricultural landscapes

[44]. Urbanization also shapes functional community structure by filtering out species according to traits that make them more or less tolerant to urban conditions; for example, energy allocation to reproduction or wingspan size for birds [45] and specific leaf area or life span for plants [46].

Combined effects

Typically, disturbances do not occur in isolation and the effect of multiple drivers on an ecosystem must be considered [30,47,48]. The combined effects of environmental changes and direct human impacts are likely to reduce greatly overall species richness and trait diversity by filtering out species not only located in different parts of the functional space, but also acting additionally, or even in synergy, leading to rapid extinctions when their effects overlap in functional space (Figure 2e). For instance, fishing pressure and climate change may impact different fish species according to their traits. Indeed, species that are small and with a short life span responded quickly to changing climates, whereas larger species declined due to size-selective overharvesting [26].

The combined effects of environmental changes and biotic pressure may also result in a change of functional community structure by provoking the decline of species in different parts of the functional space. The fish community in the Colorado River Basin was influenced by both modified environmental conditions and biotic pressure from non-native species [33]. Thus, native communities may experience two combined pressures mediated by functional traits: species were filtered out due to either vulnerable traits associated with environmental changes or competition with non-native species sharing similar traits [33].

Clearly, the functional space occupied by communities can be modified in different ways under varied disturbances that may act on species occurrences and abundances. To embrace the full range of these modifications, we need to rely on appropriate and complementary quantitative tools that may, alone or in combination, reveal non-random and directional changes in functional community structure along disturbance gradients.

Assessing changes in functional community structure Complementary indices

The common step to all functional ecology studies is to characterize the functional strategy of each species of interest by identifying a relevant combination of functional traits (Figure 1) [49–51]. It is then possible to build a multidimensional functional space with axes corresponding to raw functional traits or to synthetic traits summarizing several raw traits (e.g., after using a principal component analysis or a principal coordinate analysis) [52,53]. Quantifying the functional structure of communities involves describing the distribution of points (i.e., species) and of their weights (i.e., abundances) in this multidimensional Euclidean space. These distributions cannot be summarized using only one index because the functional structure of communities embraces several complementary components (Box 2). However, some synthetic indices exist, such as the quadratic entropy index [54],

which combines the richness, evenness, and divergence components of functional diversity [55] and which can be decomposed across hierarchical factors [56,57], that is, decomposed across different levels of variation usually along a spatial or temporal scale. This index is widely used to reveal not only phylogenetic and functional assembly rules in ecological communities [56], but also historical and biogeographic processes shaping species assemblages at larger scales [58]. Here, we present a non-exhaustive set of complementary indices that are appropriate for a broad range of ecological contexts (Box 2).

Monotonic relation with disturbance

The rationale behind the use of these components, instead of classical taxonomic-based diversity indices, to reveal impact of disturbances on community structure is that they are likely to show consistent monotonic relations along disturbance gradients [59]. By contrast, taxonomic-based indices mostly show unimodal or idiosyncratic relations [60–62] (Box 3). For instance, species richness is assumed to peak for intermediate disturbance levels and, thus, is unable to unravel low and high disturbance levels, whereas functional richness, through trait filtering,

Box 2. Practical tools for assessing changes in the functional structure of ecological communities after disturbance

We present several indices capable of tracking change in different complementary components of functional community structure (Figure 1), as well as functions implemented in the R software to compute them (Table 1). In addition, we provide the function

FSEChange (see the supplementary material online) that calculates all indices presented in Figure 1 and gives details about loser and winner species (in terms of abundance after disturbance).

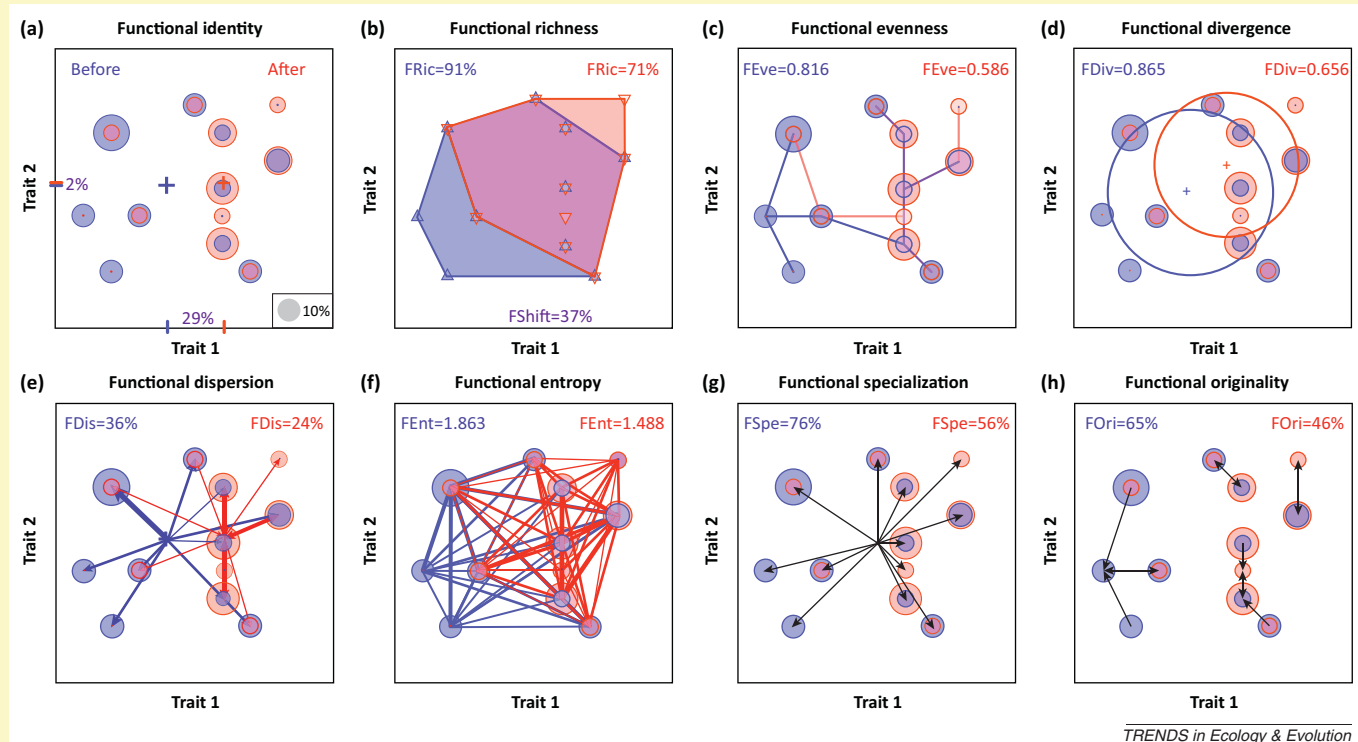


Figure 1. Potential changes in different components of the functional structure of species communities after disturbance. Species (dots) are plotted in two-dimensional functional space according to their respective trait values, where axes are quantitative traits or synthetic traits extracted from a principal component analysis (PCA) or principal coordinate analysis (PCoA) [52,53]. Circle sizes are proportional to species relative abundances before and after disturbance in blue and red, respectively. (a) Changes in species abundances may change the functional identity (mean values of traits as crosses) of species communities (i.e., abundance-weighted average value for each trait [99]), illustrated on each functional space axis by colored bars. Here, the mean trait value of the assemblage increases after disturbance for trait 1, but does not change markedly for trait 2. (b) Changes in species composition may modify the functional richness (FRic; i.e., the portion of the functional space filled by species communities [52,59]), as illustrated by the change in the convex surface gathering all the species belonging to the community. Here, functional richness is eroded after disturbance. The overall shift in the functional space can be estimated using the percentage overlap between the pre- and post-disturbance convex surfaces. Here, the portion of the functional space filled only by the pre- or post-disturbance assemblage represents 37% of their combined volume. (c) Changes in functional evenness (FEve) measure the modifications in the regularity of abundance distributions in the functional space (along the shortest minimum spanning tree linking all the species) [52]. Here, functional evenness decreases after disturbance. (d) Changes in functional divergence (FDiv) reflect changes in the proportion of the total abundance that is supported by the species with the most extreme functional traits [52] (i.e., far from the center of the functional space filled by the community), here the two colored crosses in the middle of the circle, which represent the mean functional distance from the center for each community. In this example, functional divergence decreases after disturbance. (e) Changes in functional dispersion reflect changes in the abundance-weighted deviation of species trait values from the center of the functional space filled by the community (i.e., the abundance-weighted mean distance to the abundance-weighted mean trait values of the community [53]). Line width is proportional to species abundance. Here, functional dispersion decreases after disturbance. (f) Changes in functional entropy (Rao index) reflect changes in the abundance-weighted sum of pairwise functional distances between species [54]. Line width is proportional to the total abundance of species pairs. This index needs to be expressed as an equivalent number of species to be comparable between communities [57]. Here, functional entropy decreases after disturbance. (g) Changes in functional specialization (FSpe) show how generalist species (i.e., species close to the center of the functional space, here linking all species) or specialist species (i.e., having extreme trait combinations) tend to increase in abundance [62]. In this example, functional specialization decreases after disturbance because specialists are relatively less abundant compared with generalist species. (h) Changes in functional originality (FOr) quantifies how changes in species abundances modify the functional redundancy between species (i.e., black lines are minimal functional distances among species pairs) [78]. Here, species tend to be functionally less original in the pool after disturbance because they tend to share their traits more closely with other species.

Table I. List of functions from R libraries to compute indices and assess changes in functional community structure

Main goal	Specific action	R function	R library
Building the functional space	Standardize continuous traits	<i>scale</i>	base
	Reduce space dimensionality (PCA)	<i>dudi.pca</i>	ade4
	Distance between species for qualitative traits or when missing values (Gower)	<i>daisy</i>	cluster
	Synthetic axes from any distance measure (PCoA)	<i>pcoa</i>	ape
Calculating indices of functional community structure	Functional identity or community-weighted mean trait values	<i>functcomp</i>	FD
	Functional diversity indices (functional richness, evenness, divergence, dispersion, entropy: Rao)	<i>dbFD</i>	FD
Assessing change in functional community structure	Functional dissimilarity using community overlap in the functional space	<i>all.intersect</i>	rccd
	Randomly permuting species abundances and/or occurrences for null models	<i>sample</i>	base
	Trait–environment relations (RLQ analysis)	<i>rlq</i>	ade4
	Predicting functional community structure (MaxEnt analysis)	<i>maxent</i>	FD

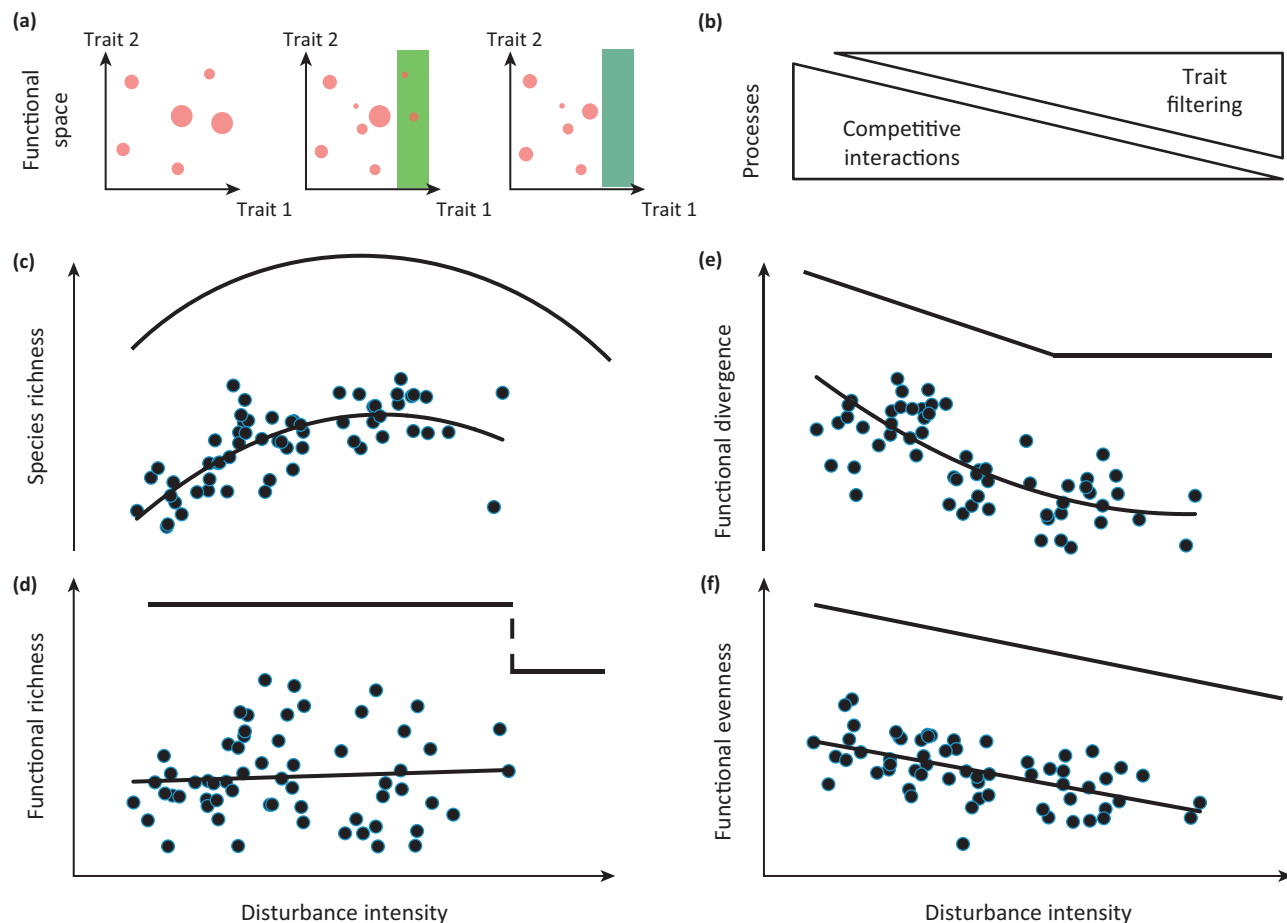
is expected to decrease for high disturbance levels when species are filtered out [59,63]. We also argue that indices based on both species traits and abundances (e.g., functional divergence or specialization) are more likely to act as early-warning indicators because they do not need species extirpations or local extinctions to change monotonically along disturbance gradients [62]. Indeed, under the assumption that the environment determines the performance of species according to their combinations of traits (performance filter hypothesis), even low disturbance intensity may deplete populations of species with vulnerable combinations of traits without modifying species composition and, thus, without affecting species and functional richness (Box 3).

Statistical tests
Changes in the functional structure of communities before and after disturbance can be assessed by estimating and comparing indices of functional community structure (Box 2) or by estimating the dissimilarity between these structures, which has been extensively called functional β -diversity or functional turnover between communities [57,64]. The first approach requires statistical tests to assess differences in index values or, more often, null models, because strong correlations may occur between functional and taxonomic structure of communities [63,65]. The second is based on a measure of dissimilarity that can be estimated using the overlap of communities before and after disturbance in the functional space [13], or by decomposing indices into α , β , and γ components across space or

Box 3. A theoretical basis and empirical evidence for monotonic changes in the functional structure of ecological communities along a disturbance gradient

Here, we present a potential mechanistic basis and an empirical example to show how the indices quantifying the various components of functional community structure might vary monotonically with the intensity of disturbance. whereas taxonomic-based indices do not. Furthermore, this example shows how functional indices could provide early warning signals of disturbance impacts. First, we present a hypothetical functional space where eight species are placed (Figure 1a). We illustrate how a disturbance, which affects species with the highest values for trait 1 (trait filtering process), may modify four indices (Figure 1b). Our theoretical example assumes that species richness shows a unimodal and, thus, a non-monotonic relation with disturbance (Figure 1c), in accordance with the intermediate disturbance hypothesis (IDH). When the disturbance intensity increases, the populations of the two species with the highest values for trait 1 are depleted, whereas the two species with medium to low values for trait 1 colonize the community. Functional richness shows a delayed response along the disturbance gradient because its decrease requires local extinction of species with extreme combinations of traits (Figure 1d). Here, it would decrease after the extinction of the two species having the highest trait 1 values because the functional space occupied by the community would be abruptly eroded. By contrast, functional divergence displays an early and rapid decreasing relation along the disturbance gradient (Figure 1e) due to declining abundance of the specialist species that are most impacted by the disturbance (those with high values for trait 1 in this example). After the extinction event, functional divergence is expected to stabilize because the remaining species do not experience any disturbance. Functional evenness shows a continuous decline with increasing disturbance intensity (Figure 1f). Indeed, at low disturbance levels, the influence of

competitive interactions on community structure relative to disturbance-based trait filtering should be high. According to limiting similarity theory [83], only species with dissimilar combinations of traits would coexist. In this situation, dissimilar species can maintain similar abundances and even distributions throughout functional space. When disturbance intensity increases, the influence of trait filtering increases relative to limiting similarity, potentially causing co-occurring species to become more clustered in functional space, thus decreasing functional evenness. In addition, species abundances have uneven distributions in functional space because disturbance is affecting only species with particular traits. The balance between competitive interactions and trait filtering can thus drive a progressive decrease in functional evenness along a disturbance gradient.
Using published data (ground beetle communities disturbed by flooding), we show that empirical patterns can follow these theoretical predictions. Communities accumulate species when disturbance intensity increases from low to moderate levels according to the IDH. These new species do not bring new combinations of traits, because their addition does not cause an increase in functional richness. Rather, it increases redundancy because more species are packed into a constant volume of functional space. This increase in redundancy causes declines in functional divergence and functional evenness. In the empirical example, functional richness does not decline because the disturbance intensity is not strong enough to cause the local extinction of species with extreme trait values. Conversely, functional divergence and evenness, by incorporating quantitative abundance data, provide an early warning signal of disturbance impacts, even though species richness is not monotonically related to disturbance intensity.



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Figure 1. Theoretical changes in the structure of a species community along a disturbance gradient. **(a)** Species (circles) are plotted in a two-dimensional functional space according to their respective trait values and circle sizes are proportional to species abundances. Arbitrarily, disturbance (light to dark green along the gradient) depletes the populations of species with the highest trait 1 values until local extinction. **(b)** Along this disturbance gradient, species would interact and replace each other: that is, competitive interactions and trait filtering. The theoretical relations between species richness **(c)**, three functional diversity indices **(d–f)** and the disturbance level are interlaced with empirical data from ground beetle communities sampled along a gradient of flood disturbance in grasslands (Elbe River, Germany) [100]. Data were fitted using generalized linear mixed effects models for linear, quadratic, and logarithmic relations. Species richness shows a unimodal shape, functional richness has no relation with disturbance intensity, and functional divergence displays a decreasing logarithmic relation, whereas functional evenness decreases proportionally with disturbance intensity. Adapted from [100].

time [57,64,66], with β measuring the amount of difference in functional trait distributions before and after disturbance. Here again, null models randomizing species abundances, occurrences or traits are necessary to test statistically the significance of dissimilarity or β -diversity values along disturbance gradients independently of changes in taxonomic composition [13,64,66].

A predictive framework

Beyond statistical tests assessing changes in functional community structure, the next challenge is to predict accurately the functional structure of communities under future disturbances. Some quantitative tools to develop such a predictive ecology are promising, such as those linking mean functional identity to disturbance based on either the three-table ordination method (called RLQ) [67] or the fourth-corner analysis [68]. The latter method has been extended to include species abundances [69] and has been successfully used to link the functional structure of communities to various types of disturbance, such as fire

[70], logging [71], or flooding [72]. The linear trait-environment (LTE) method, a linear counterpart to the fourth-corner analysis, relies on multivariate linear regressions for species-site relations and has been recently used to explore the relation between bird population dynamics and climate change [73]. The partial RLQ method has been proposed to avoid confounding effects caused by covariables that may blur trait–environment correlations by partitioning environmental heterogeneity in the RLQ method [74]. With this approach, the effect of grazing on plant traits, such as leaf size, dispersal, and rhizomatous growth, has been demonstrated after removing environmental variation caused by habitats and years [74].

Given that disturbances are likely to increase in intensity and frequency in the near future, modeling tools aiming to predict the functional structure of communities will enable drastic shifts in ecosystem functioning to be anticipated. For instance, the Maximum Entropy (MaxEnt) model, using a performance filter, posits that the relative abundance of every species in a given

environment is a function of their trait values [75]. The MaxEnt model was used to predict community-weighted mean trait values along a broad climatic gradient (a range of 12 °C for mean annual temperature) in upland forest communities of the southwestern USA [42]. It was found that environmental factors explained between 31% and 74% of the forest community-weighted mean trait values. This study paves the way, through strong trait–environment relations, toward a trait-based model of community assembly to better forecast shifts in species distributions in a warmer climate and associated shifts in functional community structure.

Concluding remarks

Traditionally, ecologists have explored linkages between the severity and type of disturbance and taxonomic composition of communities, with species richness, evenness, or population abundance often being the sole descriptors [61]. However, the number of species maintained by a community is the result of different combinations of factors acting at various temporal and spatial scales [76]. As a result, these community descriptors are often weak quantitative tools in monitoring studies because different processes may affect species in different ways, potentially providing no signal of disturbance [77], or even a false signal of ecosystem recovery [62]. Here, we synthesized evidence that the functional structure of ecological communities, through an analysis of their functional traits, provides a framework capable of detecting different types of disturbance. These techniques may be useful discriminators of disturbance effects even where community composition is modified only marginally [78], where trait–environment linkages are weak [20], and where functional diversity remains stable [79]. An analysis of functional space provides a basis for detecting changes in ecosystems that is independent of taxonomic structures or total richness. It measures changes not only to the ecosystem, but also to the species involved [80] and, as such, needs to be considered in applied studies that aim to evaluate management success [81]. However, the level of competitive interactions within communities, which remains controversial along disturbance gradients [82], may blur the influence of disturbance on the functional structure of communities because, under competition, only species with dissimilar combinations of traits would coexist [83] counteracting the disturbance-based trait filtering that increases with disturbance intensity.

Most exciting of all, analyses of functional traits offer the potential for advanced warning [62] because they can detect disturbance impacts before species loss and extinctions occur (Box 3). Indeed, species abundance distributions are expected to be modified deterministically in the functional space after disturbance, with species having combinations of traits under pressure losing abundance, whereas the others may remain stable. Given that these abundance changes will occur before local extinctions, reductions in functional divergence and evenness, which both reflect abundance distributions in the functional space, will reveal disturbance impacts earlier than will functional richness (Box 3, Figure I). Ultimately, if the link between trait combinations and sensitivity to disturbance

could be assessed accurately, a predictive ecology of disturbance may be developed that can anticipate which species will be depleted first [42,84]. This would also need to integrate the level of competitive interactions along a disturbance gradient [82], the knowledge of trait-mediated population dynamics, and other processes, such as the dynamic equilibrium model [85]. These kinds of result can pave the way toward predictive trait-based indicators of shifts in ecosystem functioning [86,87]. In a world where novel ecosystems, assemblages, and communities are increasingly prevalent, trait space offers clear insights into the way that ecosystems are changing and what the future may hold for the ecosystems of the world.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.jtree.2012.10.004>.

References

- 1 Worm, B. and Tittensor, D.P. (2011) Range contraction in large pelagic predators. *Proc. Natl. Acad. Sci. U.S.A.* 108, 11942–11947
- 2 Visconti, P. *et al.* (2011) Future hotspots of terrestrial mammal loss. *Philos. Trans. R. Soc. B* 366, 2693–2702
- 3 Maclean, I.M.D. and Wilson, R.J. (2011) Recent ecological responses to climate change support predictions of high extinction risk. *Proc. Natl. Acad. Sci. U.S.A.* 108, 12337–12342
- 4 Hermoso, V. *et al.* (2011) Invasive species and habitat degradation in Iberian streams: an analysis of their role in freshwater fish diversity loss. *Ecol. Appl.* 21, 175–188
- 5 Cardinale, B.J. *et al.* (2012) Biodiversity loss and its impact on humanity. *Nature* 486, 59–67
- 6 Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310
- 7 Bongers, F. *et al.* (2009) The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecol. Lett.* 12, 798–805
- 8 Svensson, J.R. *et al.* (2009) Equal rates of disturbance cause different patterns of diversity. *Ecology* 90, 496–505
- 9 dos Santos, F.A.S. *et al.* (2011) Neutral communities may lead to decreasing diversity–disturbance relationships: insights from a generic simulation model. *Ecol. Lett.* 14, 653–660
- 10 Kadmon, R. and Benjamini, Y. (2006) Effects of productivity and disturbance on species richness: a neutral model. *Am. Nat.* 167, 939–946
- 11 Hubbell, S.P. (2001) *The Unified Theory of Biodiversity and Biogeography*, Princeton University Press
- 12 Weiher, E. *et al.* (2011) Advances, challenges and a developing synthesis of ecological community assembly theory. *Philos. Trans. R. Soc. B* 366, 2403–2413
- 13 Villeger, S. *et al.* (2011) The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol. Lett.* 14, 561–568
- 14 Houseman, G.R. and Gross, K.L. (2011) Linking grassland plant diversity to species pools, sorting and plant traits. *J. Ecol.* 99, 464–472
- 15 Edwards, K.F. *et al.* (2011) Evidence for a three-way trade-off between nitrogen and phosphorus competitive abilities and cell size in phytoplankton. *Ecology* 92, 2085–2095

Review

Trends in Ecology and Evolution xxx xxxx, Vol. xxx, No. x

- 16 Venn, S.E. *et al.* (2011) Using plant functional traits to explain community composition across a strong environmental filter in Australian alpine snowpatches. *Plant Ecol.* 212, 1491–1499
- 17 Holt, R.D. (1985) Density-independent mortality, non-linear competitive interactions, and species coexistence. *J. Theor. Biol.* 116, 479–493
- 18 Haddad, N.M. *et al.* (2008) Species' traits predict the effects of disturbance and productivity on diversity. *Ecol. Lett.* 11, 348–356
- 19 Pakeman, R.J. (2011) Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology* 92, 1353–1365
- 20 Sonnier, G. *et al.* (2010) Quantifying relationships between traits and explicitly measured gradients of stress and disturbance in early successional plant communities. *J. Veg. Sci.* 21, 1014–1024
- 21 Naeem, S. *et al.* (2012) The functions of biological diversity in an age of extinction. *Science* 336, 1401–1406
- 22 Ricklefs, R.E. (2005) Small clades at the periphery of passerine morphological space. *Am. Nat.* 165, 651–659
- 23 Friedman, M. (2009) Ecomorphological selectivity among marine teleost fishes during the end-Cretaceous extinction. *Proc. Natl. Acad. Sci. U.S.A.* 106, 5218–5223
- 24 Olden, J.D. *et al.* (2007) Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes. *Global Ecol. Biogeogr.* 16, 694–701
- 25 Myers, R.A. and Worm, B. (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283
- 26 Genner, M.J. *et al.* (2010) Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biol.* 16, 517–527
- 27 Kantoussan, J. *et al.* (2010) Ecological indicators based on trophic spectrum as a tool to assess ecosystems fishing impacts. *Ecol. Indic.* 10, 927–934
- 28 McClenachan, L. (2009) Documenting loss of large trophy fish from the Florida Keys with historical photographs. *Conserv. Biol.* 23, 636–643
- 29 Luiz, O.J. and Edwards, A.J. (2011) Extinction of a shark population in the Archipelago of Saint Paul's Rocks (equatorial Atlantic) inferred from the historical record. *Biol. Conserv.* 144, 2873–2881
- 30 Graham, N.A.J. *et al.* (2011) Extinction vulnerability of coral reef fishes. *Ecol. Lett.* 14, 341–348
- 31 Brewer, T.D. *et al.* (2009) Thresholds and multiple scale interaction of environment, resource use, and market proximity on reef fishery resources in the Solomon Islands. *Biol. Conserv.* 142, 1797–1807
- 32 Corbin, J.D. and D'Antonio, C.M. (2010) Not novel, just better: competition between native and non-native plants in California grasslands that share species traits. *Plant Ecol.* 209, 71–81
- 33 Olden, J.D. *et al.* (2006) Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecol. Monogr.* 76, 25–40
- 34 Brown, P.M.J. *et al.* (2011) Decline in native ladybirds in response to the arrival of *Harmonia axyridis*: early evidence from England. *Ecol. Entomol.* 36, 231–240
- 35 Coomes, D.A. *et al.* (2003) Factors preventing the recovery of New Zealand forests following control of invasive deer. *Conserv. Biol.* 17, 450–459
- 36 Mason, N.W.H. *et al.* (2010) Stand development moderates effects of ungulate exclusion on foliar traits in the forests of New Zealand. *J. Ecol.* 98, 1422–1433
- 37 Brown, J.H. *et al.* (1997) Reorganization of an arid ecosystem in response to recent climate change. *Proc. Natl. Acad. Sci. U.S.A.* 94, 9729–9733
- 38 Brando, P.M. *et al.* (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biol.* 18, 630–641
- 39 Breshears, D.D. *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *Proc. Natl. Acad. Sci. U.S.A.* 102, 15144–15148
- 40 Allen, C.D. *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *For. Ecol. Manage.* 259, 660–684
- 41 Hacke, U.G. *et al.* (2001) Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. *Oecologia* 126, 457–461
- 42 Laughlin, D.C. *et al.* (2011) Climatic constraints on trait-based forest assembly. *J. Ecol.* 99, 1489–1499
- 43 Owens, I.P.F. and Bennett, P.M. (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proc. Natl. Acad. Sci. U.S.A.* 97, 12144–12148
- 44 Duchamp, J.E. and Swihart, R.K. (2008) Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landscape Ecol.* 23, 849–860
- 45 Croci, S. *et al.* (2008) Does urbanization filter birds on the basis of their biological traits? *Condor* 110, 223–240
- 46 Vallet, J. *et al.* (2010) Using biological traits to assess how urbanization filters plant species of small woodlands. *Appl. Veg. Sci.* 13, 412–424
- 47 Statzner, B. and Beche, L.A. (2010) Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshw. Biol.* 55, 80–119
- 48 Crain, C.M. *et al.* (2008) Interactive and cumulative effects of multiple human stressors in marine systems. *Ecol. Lett.* 11, 1304–1315
- 49 Keddy, P.A. (1992) Assembly and response rules: 2 goals for predictive community ecology. *J. Veg. Sci.* 3, 157–164
- 50 Petchey, O.L. and Gaston, K.J. (2006) Functional diversity: back to basics and looking forward. *Ecol. Lett.* 9, 741–758
- 51 Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
- 52 Villegger, S. *et al.* (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301
- 53 Laliberté, E. and Legendre, P. (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305
- 54 Botta-Dukat, Z. (2005) Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.* 16, 533–540
- 55 Mouchet, M.A. *et al.* (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876
- 56 Pavoine, S. and Bonsall, M.B. (2011) Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.* 86, 792–812
- 57 Ricotta, C. and Szeidl, L. (2009) Diversity partitioning of Rao's quadratic entropy. *Theor. Popul. Biol.* 76, 299–302
- 58 Meynard, C.N. *et al.* (2011) Beyond taxonomic diversity patterns: how do alpha, beta and gamma components of bird functional and phylogenetic diversity respond to environmental gradients across France? *Global Ecol. Biogeogr.* 20, 893–903
- 59 Cornwell, W.K. *et al.* (2006) A trait-based test for habitat filtering: convex hull volume. *Ecology* 87, 1465–1471
- 60 Alcock, K.G. and Hik, D.S. (2003) What determines disturbance–productivity–diversity relationships? The effect of scale, species and environment on richness patterns in an Australian woodland. *Oikos* 102, 173–185
- 61 Mackey, R.L. and Currie, D.J. (2001) The diversity–disturbance relationship: Is it generally strong and peaked? *Ecology* 82, 3479–3492
- 62 Villegger, S. *et al.* (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* 20, 1512–1522
- 63 Flynn, D.F.B. *et al.* (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecol. Lett.* 12, 22–33
- 64 de Bello, F. *et al.* (2010) The partitioning of diversity: showing Theseus a way out of the labyrinth. *J. Veg. Sci.* 21, 992–1000
- 65 Petchey, O.L. *et al.* (2007) Low functional diversity and no redundancy in British avian assemblages. *J. Anim. Ecol.* 76, 977–985
- 66 Ackerly, D.D. and Cornwell, W.K. (2007) A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.* 10, 135–145
- 67 Doledec, S. *et al.* (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environ. Ecol. Stat.* 3, 143–166
- 68 Legendre, P. *et al.* (1997) Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology* 78, 547–562
- 69 Dray, S. and Legendre, P. (2008) Testing the species traits–environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412

- 70 Huebner, K. *et al.* (2012) Post-fire succession of collembolan communities in a northern hardwood forest. *Eur. J. Soil Biol.* 48, 59–65
- 71 Azeria, E.T. *et al.* (2011) Differential response of bird functional traits to post-fire salvage logging in a boreal forest ecosystem. *Acta Oecol.* 37, 220–229
- 72 Gallardo, B. *et al.* (2009) Testing the response of macroinvertebrate functional structure and biodiversity to flooding and confinement. *J. Limnol.* 68, 315–326
- 73 Cormont, A. *et al.* (2011) Using life-history traits to explain bird population responses to changing weather variability. *Clim. Res.* 49, 59–71
- 74 Wesuls, D. *et al.* (2012) Disentangling plant trait responses to livestock grazing from spatio-temporal variation: the partial RLQ approach. *J. Veg. Sci.* 23, 98–113
- 75 Shipley, B. *et al.* (2006) From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science* 314, 812–814
- 76 Scheiner, S.M. *et al.* (2011) The underpinnings of the relationship of species richness with space and time. *Ecol. Monogr.* 81, 195–213
- 77 Hussin, W.M.R.W. *et al.* (2012) Impacts of physical disturbance on the recovery of a macrofaunal community: a comparative analysis using traditional and novel approaches. *Ecol. Indic.* 12, 37–45
- 78 Mouillot, D. *et al.* (2008) Do we protect biological originality in protected areas? A new index and an application to the Bonifacio Strait Natural Reserve. *Biol. Conserv.* 141, 1569–1580
- 79 Loiola, P.D. *et al.* (2010) Functional diversity of herbaceous species under different fire frequencies in Brazilian savannas. *Flora* 205, 674–681
- 80 Diaz, S. *et al.* (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc. Natl. Acad. Sci. U.S.A.* 104, 20684–20689
- 81 Cadotte, M.W. (2011) The new diversity: management gains through insights into the functional diversity of communities. *J. Appl. Ecol.* 48, 1067–1069
- 82 Schamp, B.S. and Aarssen, L.W. (2009) The assembly of forest communities according to maximum species height along resource and disturbance gradients. *Oikos* 118, 564–572
- 83 MacArthur, R. and Levins, R. (1967) Limiting similarity convergence and divergence of coexisting species. *Am. Nat.* 101, 377–387
- 84 Dziock, F. *et al.* (2011) Reproducing or dispersing? Using trait based habitat templet models to analyse Orthoptera response to flooding and land use. *Agric. Ecosyst. Environ.* 145, 85–94
- 85 Huston, M. (1979) General hypothesis of species-diversity. *Am. Nat.* 113, 81–101
- 86 Suding, K.N. *et al.* (2008) Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biol.* 14, 1125–1140
- 87 Lavorel, S. and Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556
- 88 Wainwright, P.C. (1994) Functional morphology as a tool on ecological research. In *Morphology: Integrative Organismal Biology* (Wainwright, P.C. and Reilly, S.M., eds), pp. 42–59, The University of Chicago Press
- 89 Gatz, A.J. (1979) Community organization in fishes as indicated by morphological features. *Ecology* 60, 711–718
- 90 James, F.C. (1982) The ecological morphology of birds: a review. *Ann. Zool. Fenn.* 19, 265–275
- 91 Albouy, C. *et al.* (2011) Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology. *Mar. Ecol. Prog. Ser.* 436, 17–28
- 92 Winemiller, K.O. (1991) Ecomorphological diversification in lowland fresh-water fish assemblages from 5 biotic regions. *Ecol. Monogr.* 61, 343–365
- 93 Bapst, D.W. *et al.* (2012) Graptoloid diversity and disparity became decoupled during the Ordovician mass extinction. *Proc. Natl. Acad. Sci. U.S.A.* 109, 3428–3433
- 94 Norberg, U.M. (1994) Wing design, flight performance, and habitat use in bats. In *Morphology: Integrative Organismal Biology* (Wainwright, P.C. and Reilly, S.M., eds), pp. 205–239, The University of Chicago Press
- 95 Poff, N.L. *et al.* (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *J. N. Am. Benthol. Soc.* 25, 730–755
- 96 Diaz, S. and Cabido, M. (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655
- 97 Bellwood, D.R. *et al.* (2006) Functional versatility supports coral reef biodiversity. *Proc. R. Soc. Lond. B: Biol. Sci.* 273, 101–107
- 98 Dulvy, N.K. *et al.* (2004) Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can. J. Fish. Aquat. Sci.* 61, 466–475
- 99 Garnier, E. *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637
- 100 Gerisch, M. *et al.* (2012) More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos* 121, 508–515