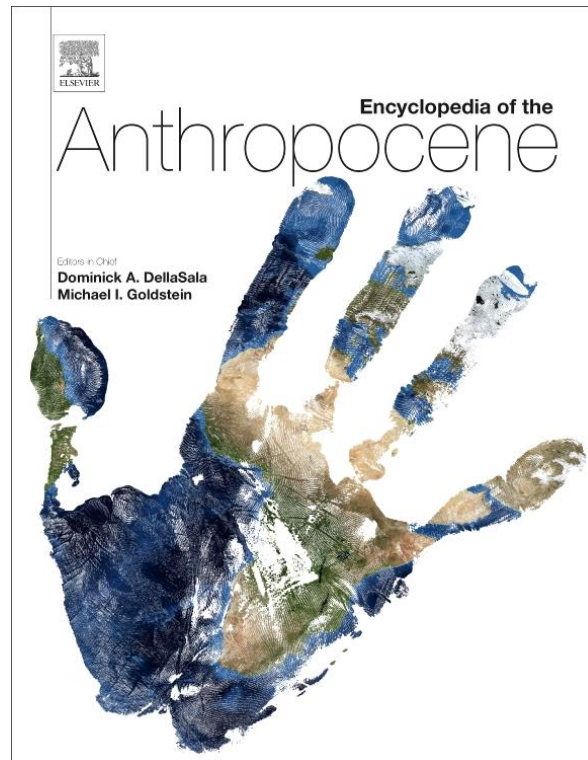


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Willig M.R., and Presley S.J. (2018) Biodiversity and Disturbance. In: Dominick A. DellaSala, and Michael I. Goldstein (eds.) *The Encyclopedia of the Anthropocene*, vol. 3, p. 45-51. Oxford: Elsevier.

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## Biodiversity and Disturbance

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### Introduction

The identities and abundances of species at any particular site vary over time. Similarly, the identities and abundances of species vary over space at any point in time. Such spatiotemporal variation in biodiversity represents a foundational ecological characteristic from both theoretical and empirical perspectives (Scheiner and Willig, 2011) and is a result of the effects of disturbance regimes on biodiversity, primarily as a consequence of patch dynamics and ecological succession (see Pickett and White, 1985; Pickett et al., 1999, 2011). During succession, biodiversity and species composition change due to species-specific niche requirements, as well as because of differences among species in competitive ability, colonization ability, and their trade-offs. Moreover, the terms “biodiversity” and “disturbance” can each have multiple meanings and measures that are contextualized or operationalized with regard to spatial scale, sometimes leading to ambiguity and confusion. Consequently, we briefly introduce the concepts of biodiversity, disturbance, and succession, as well as their scale sensitivity, and then explore linkages from temporal and spatial perspectives.

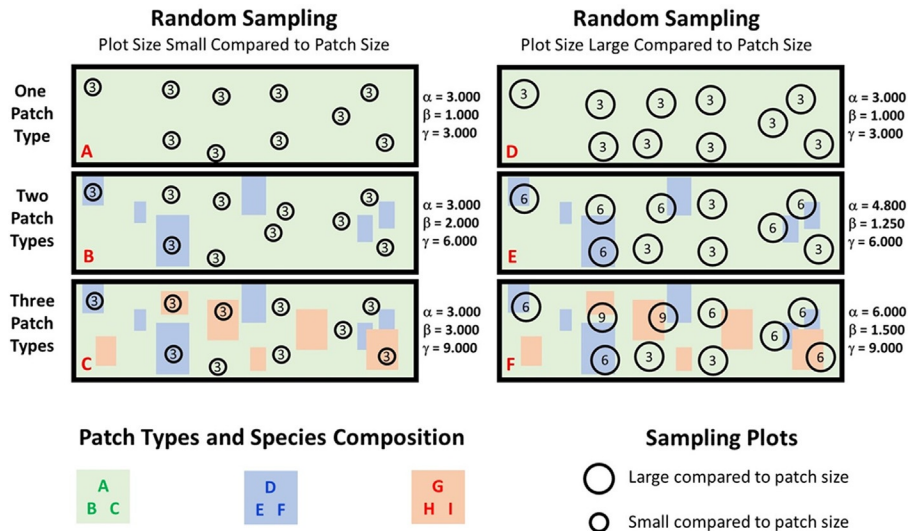
### Biodiversity

At its simplest, biodiversity is “the variety of life” (Wilson, 1988). Nonetheless, this simplicity conceals a more complex and multidimensional meaning. For example, biodiversity can be applied at a number of levels in an ecological hierarchy (e.g., from individuals, to populations or communities, to the biosphere), in an evolutionary hierarchy (e.g., from genes, to individuals, to populations, to species, to higher taxonomic designations), or in a spatial hierarchy (e.g., from patches, to landscapes, to regions). Moreover, it can reflect a variety of species attributes including differences related to the “importance” (i.e., abundance, biomass, or frequency of occurrence), functional characteristics (e.g., where an organism forages, when it is active, how it obtains food, and what kinds of food it consumes), or evolutionary history (e.g., evolutionary relationships or positions on a phylogenetic tree) of species (Faith, 1992; Webb et al., 2002; Cavender-Bares et al., 2009; Pavoine and Bonsall, 2011). Although most macroecological or biogeographic research on biodiversity has focused on species richness, ecological research has increasingly considered abundance diversity (e.g., species evenness, species diversity) as well. More recently, functional and phylogenetic aspects of biodiversity have become the focus of considerable ecological and biogeographic research from both theoretical and empirical perspectives. Herein we primarily consider species richness, in part because the conceptual bases for the linkage of other metrics of biodiversity to disturbance are less well developed (e.g., Svensson et al., 2011).

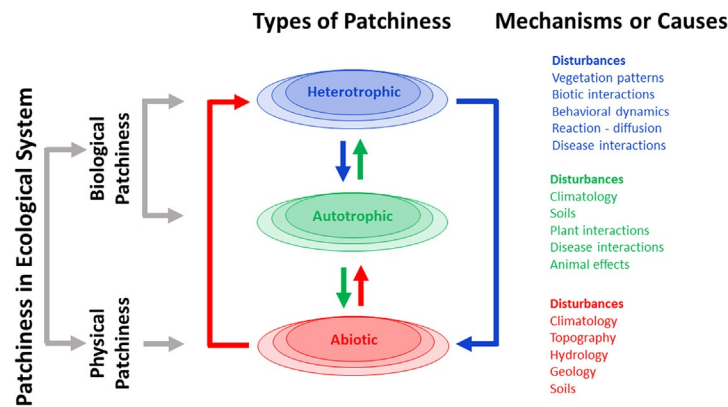
Within any spatial domain (Fig. 1) of interest (e.g., a forest plot, a stream reach, an island or lake), the total biodiversity ( $\gamma$  level) depends on (1) average biodiversity within defined focal areas ( $\alpha$  level) and (2) the differences among such focal areas ( $\beta$  level) in species composition (Gering and Crist, 2002; Cornell et al., 2007; Pegg and Taylor, 2007). The association between  $\alpha$ -level,  $\beta$ -level, and  $\gamma$ -level biodiversity is expressed in one of two models. The additive model posits that  $\gamma = \alpha + \beta$ , whereas the multiplicative model posits that  $\gamma = \alpha \times \beta$ . Although both models have merits, controversy surrounds their applications. We use the multiplicative model because its  $\beta$  effectively measures the number of distinct compartments in the landscape based on considerations of species composition. Within homogeneous domains,  $\alpha$ -level and  $\gamma$ -level biodiversity should be similar, resulting in low  $\beta$ -level biodiversity (Fig. 1, Panels A and D). Within heterogeneous domains in which different patch types harbor different species,  $\beta$ -level biodiversity should be high, and  $\alpha$ -level biodiversity should be considerably lower than  $\gamma$ -level biodiversity (Fig. 1, Panels B and C for small sampling units or Panels E and F for large sampling units). This spatial or hierarchical perspective is a critical concept for understanding how disturbances affect biodiversity and its subsequent changes during ecological succession.

### Disturbance and Succession

A disturbance (White and Pickett, 1985; Pickett et al., 1999; Walker and Willig, 1999) is a relatively discrete event in time and space that alters the structure of ecological systems (i.e., populations, communities, or ecosystems). It can do so in a number of ways (Fig. 2; Wu and Loucks, 1995): by affecting the density, biomass, or spatial distribution of the biota (producers, consumers, and decomposers), by changing the availability and distribution of resources or substrates, or by otherwise altering the physical environment (e.g., temperature, humidity). Moreover, disturbances are a pervasive feature of terrestrial and aquatic ecosystems. Indeed, disturbances can be initiated by a variety of factors (Table 1), including those of climatic or tectonic origin, those induced by the biota, and those caused by humans. Disturbances of climatic origin include high energy storms (cyclones, hurricanes, tornadoes) and wild fires, as well as droughts and floods. Disturbances of tectonic origin include earthquakes and volcanic eruptions. Disturbances of biotic origin include a variety of phenomena such as dam construction by beavers, mound or midden



**Fig. 1** Simplified graphical representation of the effects of landscape heterogeneity as represented by the number of patch types (*green, blue, or orange shading*) on the alpha ( $\alpha$ ), beta ( $\beta$ ), and gamma ( $\gamma$ ) components of biodiversity based on a multiplicative ( $\gamma = \alpha \times \beta$ ) model. *Green shading* represents an undisturbed and homogeneous patch type. *Blue and orange shading* represents either (1) two different patch types generated by different disturbances or (2) two different patch types representing different stages in succession from the same disturbance type. All patches arbitrarily contain three species (letters) with the identities of those species differing between patches (i.e., no species in common to different patch types). Regardless of sampling plot size, the consequences of increasing disturbance-generated heterogeneity (number of patches) is reflected in increasing  $\beta$ - and  $\gamma$ -diversity. Nonetheless, if plot size is large compared to patch size, some of the variation caused by disturbance will be contained in  $\alpha$ -level measures (that sample two or more patch types), thereby diminishing  $\beta$ -level measures (compare columns within rows). Areas of circles represent sizes of sampling units; numbers within circles reflect empirical richness of the sampling unit; and all species are detected within a patch type even at the smallest grain of sampling (i.e., no false absences).



**Fig. 2** A disturbance event generates patchiness in ecological systems in a hierarchical fashion. It does so directly and via interactions with other disturbance events, as well as with additional mechanisms that cause heterogeneity with regard to the abiotic, autotrophic, and heterotrophic (consumers and decomposers) components of ecological systems. Modified from Wu, J. and Loucks, O. L. (1995). From balance of nature to hierarchical patch dynamics: a paradigm shift in ecology. *Quarterly Review of Biology* **70**, 439–466.

construction by rodents, or disease outbreaks associated with pathogens (Willig and McGinley, 1999). Humans are ecosystem engineers and are pervasive in their creation of disturbances associated with land use conversion for agriculture, housing, transportation, energy production, and waste disposal. In recognition of the inescapable influence of humans in molding the structure and functioning of the world's ecosystems, we have entered a new geological age, the Anthropocene (Steffen et al., 2003; Zalasiewicz et al., 2010).

Any particular site on the earth is subject a variety of disturbance events. For example, the ecosystems of the Caribbean and eastern seaboard of North America are strongly influenced by high energy storms and to a lesser extent by droughts (Webb, 1999; Whigham et al., 1999; Brokaw et al., 2012); those of coastal wetlands are strongly influenced by sea-level rise and human development (Keddy, 2010; Scott et al., 2014); and those of grasslands are strongly influenced by fires and droughts (Knapp et al., 1998; Laurenroth and Burke, 2008). The totality of disturbance events that affect a site is represented as its disturbance regime, which is characterized by the *frequency* (number of events per unit time), *intensity* (physical force of an event), *extent* (spatial area of

**Table 1** Classification of various terrestrial disturbance types based on their origins and the approximate extent of the earth's surface (ND = data not available) over which they operate

<i>Origin</i>	<i>Disturbance type</i>	<i>Spatial extent (percent)</i>
Tectonic	Earthquake	1
	Erosion	>50
	Volcano	1
Wind	Cyclonic storm	15
	Tornado	<1
	Tree fall	ND
Water	Drought	30
	Flood	15
	Glacier	10
Fire	Fire	>50
Biotic (non-human)	Herbivory	ND
	Invasion	ND
	Animal activity	ND
Biotic (human)	Agriculture	45
	Forestry	10
	Mineral extraction	1
	Military action	1–40 <sup>a</sup>
	Transportation	5
	Urbanization	3

<sup>a</sup>Vietnam, 40%; United States, 1%.

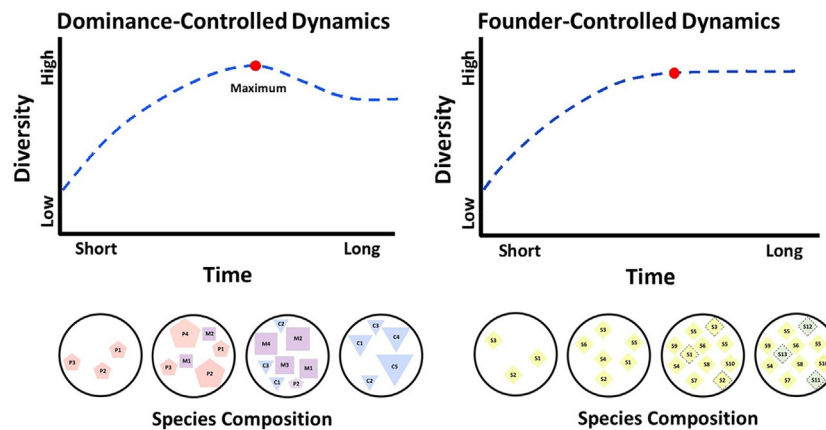
Source: Walker, L. R. and Willig, M. R. (1999). An introduction to terrestrial disturbances. In: Walker, L. R. (ed.) *Ecosystems of disturbed ground*, pp. 1–16. Amsterdam, Netherlands: Elsevier Science.

impact), and *severity* (i.e., impacts on or consequences to components of ecological systems) of each disturbance type. Finally, different disturbances may interact with each other (e.g., hurricanes increase frequency of subsequent landslides; droughts affect herbivore outbreaks, previous human land use influences the severity of subsequent hurricanes) making it difficult to isolate the effect of each disturbance in a sequence of disturbance events of the same or different type. Moreover, the effects of disturbances can be expressed at multiple levels in an ecological hierarchy (Fig. 2; Wu and Loucks, 1995) as well as in a spatially explicit manner that involves cross-scale interactions within a landscape (Peters and Havstad, 2006; Peters et al., 2007; Willig et al., 2007).

The biota responds to disturbances in a variety of ways depending on the identity and nature of the disturbance (i.e., their intensities, extents, frequencies of occurrence, and context within a landscape) and the composition of the regional species pool (i.e., the suite of potential colonists of a patch). The initial responses of the biota to a particular disturbance event are captured in the concept of severity. Importantly, the severity of a disturbance is often related to its intensity. For example, a Category 5 hurricane causes more damage to natural (forests, wetlands, reefs) and human-dominated (e.g., cities, plantations, agricultural fields) ecosystems than does a Category 3 hurricane (hurricane categories are defined by wind speed, a measure of intensity). Subsequent to initial effects, a suite of changes is induced by interactions of the biota, leading to a process known as ecological succession (Pickett et al., 2011; Pulsford et al., 2016). More specifically, succession can be thought of as the change in the ecological structure and functioning of an ecosystem over time in response to a disturbance event. Indeed, disturbances initiate succession; influence its subsequent trajectories; and can determine its rate, endpoint, and duration (Willig and Walker, 1999). Disturbances are sometimes so severe as to initiate primary succession (e.g., after the eruption of a volcano), in which case the affected areas are devoid of life (including seeds or spores). However, disturbances are generally less severe. In such less severe cases, secondary succession transpires with various residuals (e.g., seed banks in the soil, animals in well protected refugia) that remain after the impact of a disturbance affecting the tempo or mode of subsequent change (Waide and Willig, 2012).

## The Linkage Between Biodiversity and Disturbance

In general, disturbances are patch-generating or patch-modifying phenomena, and it is via these processes that biodiversity becomes associated with disturbance. In open systems that are a mosaic of patches, both interspecific interactions within patches and interpatch movement of individuals (recruits such as seeds and spores, or any immigrating individual, regardless of its stage or age) ultimately determine the composition of particular patches. As in exploiter-mediated systems (Caswell, 1978), where predators maintain the densities of competitors below critical values that would lead to local extinctions, patch generation by disturbances can have an analogous effect of reducing densities of species, including dominant taxa so that competitive interactions do not result in local extinction. Moreover, local extinctions within patches can be rescued by colonization from other patches, further mitigating Lotka–Volterra dynamics (competitive exclusion), and representing a kind of metapopulation dynamics (Hanski, 1994). Within



**Fig. 3** Graphical representation of variation in diversity as a function of time since disturbance for systems characterized by dominance-controlled dynamics (left) versus founder-controlled dynamics (right). In dominance-controlled dynamics, diversity peaks at intermediate times since disturbance (as suggested by the intermediate disturbance hypothesis) because of trade-offs between dispersal ability and competitive ability. Pioneer species (*red pentagons*, P) have highest dispersal and lowest competitive abilities; mid-successional species (*purple squares*, M) have intermediate dispersal and intermediate competitive abilities; and climax species (*blue triangles*, C) have lowest dispersal and highest competitive abilities. Thus, species composition changes in a consistent manner over time, as do the functional attributes of species, with species composition and diversity during the climax stage remaining relatively constant until disturbance alters dynamics again. In founder-controlled dynamics, no trade-off characterizes dispersal and competitive abilities, and all species (*yellow diamonds*, S) are equivalent with regard to such attributes. Thus, the arrival of species is relatively stochastic until all available space is occupied within a patch, at which time diversity stabilizes but species composition may change as a result of random patterns of death and colonization (i.e., competitive lottery for space). Gaps created by the death of individuals (*dashed lines*) allows establishment of additional species (*green shading*). In this model, species composition does not change in a consistent fashion overtime.

this general schema, a gradient of interspecific interactions or community dynamics can be identified, from *exploiter-mediated dynamics* at one extreme to *dominance-controlled dynamics* at the other extreme (Yodzis, 1986).

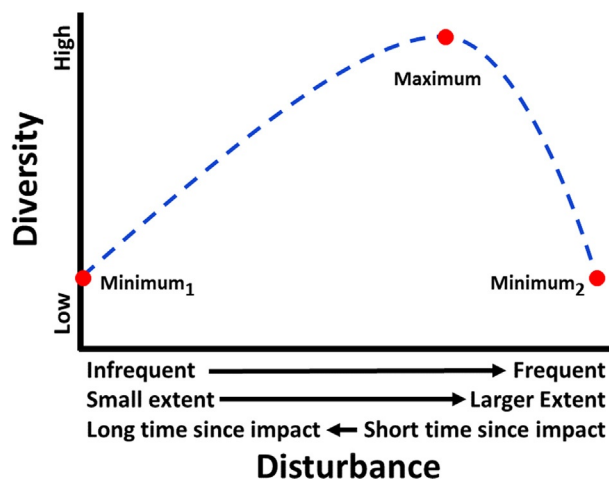
In *dominance-controlled dynamics* (Fig. 3, left panel) the regional species pool contains a mix of taxa with a spectrum of competitive and dispersal abilities. Moreover, a trade-off characterizes these abilities: good dispersers are not good interspecific competitors and good interspecific competitors are not good dispersers. This establishes a temporal dynamic for the species composition and biodiversity of a patch that can be categorized into three phases. During the first phase, mostly good dispersers (opportunistic or early successional species) reach and colonize a patch, such that richness and diversity are low. After some time, species with poorer dispersal abilities but superior competitive abilities colonize the patch, and species richness increases, representing a second phase. During the third phase, species with higher competitive abilities arrive and exclude those with poorer competitive abilities via density-dependent interactions, and species richness declines. Thus, richness is highest at intermediate time periods during succession. If the patch-generating phenomena are temporally phased over the entire landscape, as after an extensive forest fire or after an extensive flood, then the entire landscape may undergo contemporaneous successional dynamics (relatively high temporal  $\beta$ -diversity, but relatively low spatial  $\beta$ -diversity). If the patch-generating phenomena are not temporally phased, as in the case of gaps created in forest canopies due to tree-falls (in systems outside of regions prone to high energy storms) or mounds produced by rodents, then the landscape will simultaneously comprise multiple patches at different stages of succession with different species compositions and diversities (relatively low temporal turnover of species but relatively high spatial turnover of species).

In *founder-controlled dynamics* (Fig. 3, right panel), the species pool contains taxa that are equally good colonists and equally good interspecific competitors. Thus, the species composition of patches created by disturbances should not undergo temporal changes like those characteristic of succession in dominance controlled systems, as trade-offs between colonizing ability and interspecific interactions do not determine the arrival sequence or persistence of species. If patch creation by disturbance is spatially random and continuous, competitive exclusion may be less likely (i.e., a competitive lottery), especially when the number of offspring is not correlated with the biomass or productivity of the species. Even in the absence of additional disturbance, the species composition of patches will change over time only to the extent that the dying individuals are replaced by individuals of species not already present in the patch of equivalent competitive ability. This will reinforce the production of many more-or-less random assortments of species (i.e., a competitive lottery for space).

### Intermediate Disturbance Hypothesis

The intermediate disturbance hypothesis (IDH) posits that species richness (and diversity) at the local scale peaks at (1) intermediate values of disturbance frequency, (2) intermediate times after a disturbance, and (3) at intermediate spatial extents of





**Fig. 4** Simplified graphical representation of the intermediate disturbance hypothesis (Grime, 1973; Horn, 1975; Connell, 1978), which posits that diversity should be highest at intermediate levels of disturbance, and lowest at either the highest ( $\text{minimum}_2$ ) or lowest ( $\text{minimum}_1$ ) end of the disturbance gradient, depending on the characteristics of habitat represented by the extremes. In its incarnation by Connell (1978), the disturbance gradient ( $x$ -axis) could represent either the frequency or extent of a disturbance type, or the time since impact of a particular disturbance event. Note that the polarities of the frequency and extent gradient are the same (i.e., magnitude increases from left to right), whereas that of time since disturbance is reversed (i.e., recent disturbance on the right and more distant disturbance to the left). Modified from Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* **199**, 1302–1310.

disturbance (Grime, 1973; Horn, 1975; Connell, 1978). The idea is that recurrent disturbances create nonequilibrium conditions that reduce the likelihood of competitive exclusion between cooccurring species and consequently promote high species richness and diversity. These conditions are likely to occur if the time between disturbances is small compared to “rates of recovery from perturbation” (Connell, 1978). Although the IDH provided an early conceptual basis (Fig. 4) for the linkage between biodiversity and disturbance with regard to space and time, its validity from both theoretical and empirical perspectives is an ongoing controversy (see Fox, 2013a,b; Sheil and Burslem, 2013).

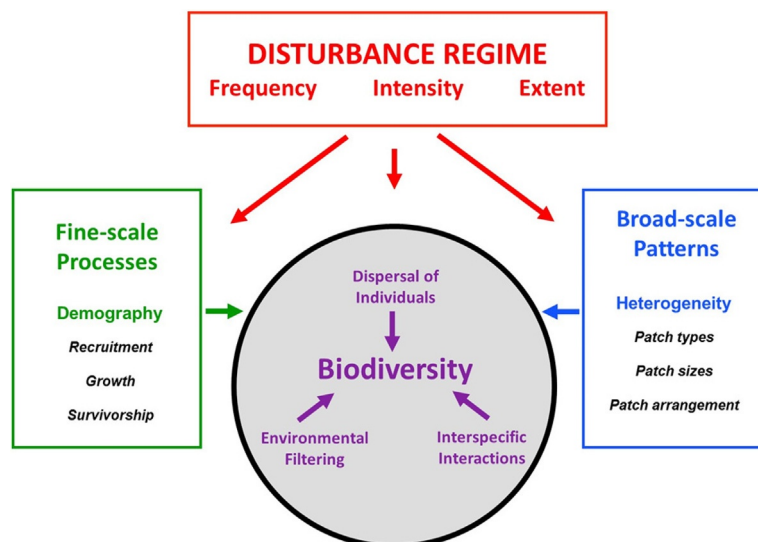
A recent review (Mackey and Currie, 2001) of published biodiversity–disturbance studies documented that from an empirical perspective, relationships are quite variable, not consistently strong and often nonsignificant, general conclusions that were corroborated by others (Hughes et al., 2007). The canonical hump-shaped pattern represented only 16.4%, 18.9%, and 10.7% of the 116 studies of species richness, 53 studies of diversity, and 28 studies of evenness, respectively. Moreover, no significant relationship was the most frequent pattern (i.e., 35.3%, 28.3%, and 50.0% of the studies of species richness, diversity, and evenness, respectively). The most frequently observed nonrandom relationships for species richness, diversity, and evenness were positive monotonic, negative monotonic, and negative monotonic, respectively. Importantly, the likelihood of detecting nonrandom relationships between biodiversity and disturbance was related to environmental characteristics of the study. For richness, significant relationships were more likely when the disturbance was not anthropogenic in origin. For diversity, significant relationships were more likely for (1) disturbances that were chronic rather than episodic, (2) studies of spatial gradients rather than temporal gradients, (3) studies that focused on disturbance intensity rather than frequency, and (4) domains comprising mosaics of patches rather than single patches or homogenous landscapes. For evenness, the likelihood of a significant relationship with disturbance was unrelated to any environmental characteristic of the study, but this conclusion must be interpreted with caution as the number of studies was small ( $N=28$ ).

Three assumptions form the conceptual foundations of the IDH (Fox, 2013a). First, disturbances reduce the abundances of species and weaken interspecific competition, thereby mitigating the likelihood of density-dependent extinction. Second, intermediate frequencies or intermediate intensities of disturbance prevent attainment of demographic equilibria by substantively reducing the densities of all species to a sufficiently low level that all of them can subsequently increase in abundance. Third, the identity of the dominant competitor changes on an intermediate time scale due to fluctuating environmental conditions associated with recurrent disturbance events such that no species has sufficient time to exert density-dependent extinction effects (all species coexist). From a theoretical perspective, Fox (2013a,b) convincingly argues that the IDH is invalid because each of its three fundamental assumptions are *logically* flawed. He suggests that theory concerning the way in which disturbance frequency and intensity affect biodiversity would be better advanced by exploring models based on nonlinearities and nonadditivities. More specifically coexisting species must exhibit negative frequency-dependence so that they tend to increase in abundance when rare and decrease in abundance when common, resulting in bounded growth. The three assumptions of the IDH do not ensure this and cannot logically lead then to long-term coexistence. Indeed, this defining characteristic can only occur with average per-capita growth rates that are nonadditive or nonlinear functions of the critical environmental characteristics to which species respond.

A recently proposed quantitative model (Miller et al., 2011) based on aspects of the disturbance regime and two-species interspecific competition suggests an alternative perspective in which the frequency and intensity of disturbance can affect biodiversity. The model is not based on the logically invalid assumptions of the IDH. Moreover, it predicts that a diversity of relationships, including hump-backed or U-shaped patterns, can characterize the relationship between biodiversity and disturbance. In essence, the model predicts that the form of the relationship between biodiversity and frequency of disturbance depends on the intensity of the disturbance. Similarly, the model predicts that the form of the relationship between biodiversity and intensity of disturbance depends on disturbance frequency. The variety of forms of the relationships that this quantitative model predicts are consistent with the variation in empirical biodiversity–disturbance relationships (Mackey and Currie, 2001; Hughes et al., 2007). This general approach holds much promise for unifying diverse observations and concepts about how biodiversity is related to the disturbance regime of a system.

## Summary

Disturbances affect biodiversity from two perspectives: a within-patch or local perspective and an among-patch or landscape perspective. From a within-patch perspective, disturbances of various frequencies or intensities can enhance local biodiversity beyond expectations based on competitive interactions. From an among-patch or landscape perspective, disturbances create heterogeneity in time and space that increases  $\beta$ -level and  $\gamma$ -level biodiversity, while rescuing species from local extinction via immigration from other patches. At virtually all scales, space is heterogeneous comprising multiple patch types, at least from the perspective of some species. These patches may arise from underlying abiotic characteristics, vegetation characteristics, heterotrophic characteristics, or their interactions (Fig. 2). At the scale of a particular patch, a disturbance event modifies the environment and affects fine-scale, demographic processes (e.g., recruitment, growth, survivorship) of constituent species, leading to changes in biodiversity (i.e., the relative abundances of species). At broader scales, disturbances create or modify the nature of patches (i.e., patch type, size, and arrangement), thereby affecting the composition and configuration of the landscape. Together these broad-scale patterns of among-patch heterogeneity combine with fine-scale demographic processes at the within-patch scale to modify biodiversity within and among patches (Fig. 5). Ultimately, the biodiversity of a patch is affected by disturbance-induced dispersal of individuals, interspecific interactions, and environmental filtering. To the extent that species-specific niche characteristics lead to different associations of taxa with different patches (enhanced  $\beta$ -level biodiversity), we expect the biodiversity of the landscape ( $\gamma$ -level biodiversity) to be related to the number of distinct patch types. Of course, even patches that were originally created by the same kind of disturbance (e.g., landslide) may be of different ages and at different stages of succession, and this will lead to further enhanced  $\beta$ -level and  $\gamma$ -level biodiversity. Finally, the movement of individuals between sites can be strongly affected by the composition and configuration of intervening patches within the landscape, which themselves have been molded by disturbance (Willig et al., 2007).



**Fig. 5** Graphical representation of mechanisms whereby cross-scale interactions determine the responses of biodiversity to the disturbance regime (modified from Willig, M. R., Bloch, C. P., Brokaw, N., Higgins, C., Thompson, J. and Zimmermann, J. (2007). Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. *Ecosystems* **10**, 824–838). The frequency, intensity, and extent of elements of the disturbance regime affect (1) a suite of fine-scale, demographic processes characteristic of the biota within patches, as well as (2) broad-scale patterns represented by the composition and configuration of patches in a landscape (landscape structure or heterogeneity). Together, these fine-scale, within-patch processes interact with broad-scale landscape structure to determine the dispersal of individuals into and out of patches, the efficacy of environmental filters, and the magnitude of interspecific interactions in mediating persistence of species and consequently biodiversity.

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