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Predicting the direction and magnitude of small mammal disturbance effects on plant diversity across scales

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Abstract. Despite years of research on small mammal disturbance effects on plant diversity, predicting the direction and magnitude of these effects remains elusive. Models such as the intermediate disturbance hypothesis, the perturbation hypothesis, or the ecosystem engineering hypothesis of small mammal disturbance, show considerable overlap but fail to account for key variable interactions and thus provide mainly *post hoc* explanations. Recent reviews have emphasized the importance of small mammals to basic and applied ecology. Re-examining the mechanisms underlying their disturbance effects is thus timely. Here I present the Slope-Hump Model, which integrates previous models and insights from the literature, and which is capable of predicting the direction and relative magnitude of disturbance effects on plant diversity. These predictions qualitatively match the results of recent meta-analyses. The model also suggests new patterns and predictions that can stimulate both pure and applied ecology research.

Keywords. Disturbance, diversity, ecosystem engineering, intermediate disturbance hypothesis, mammal, perturbation, plant, slope-hump model

Introduction

The effects of small mammal disturbances on biodiversity, especially of plants, is a recurrent topic of interest to community ecology research (Kelt 2011, Root-Bernstein and Ebensperger 2012, Davidson et al. 2012). Despite many dozens of field studies (for a meta-analysis, see Root-Bernstein and Ebensperger 2012) and several models addressing mechanisms of small mammal disturbance effects, predicting the direction and magnitude of disturbance effects on biodiversity remains elusive (Mackey and Currie 2001, Root-Bernstein and Ebensperger 2012). Existing models fail to fully explain the conditions under which they occur, ignore the role of biogeography, and incompletely account for interactions between key factors. Here I propose a simple novel model, which I designate by the original name the Slope-Hump model of disturbance. This model predicts both the relative magnitudes and directions of disturbance effects.

The first graphical model to explain the effects of disturbance was the Intermediate Disturbance Hypothesis (IDH), proposing a hump shaped relationship between disturbance and species

richness (Grime 1973, Shea et al. 2004). According to this model, at low levels of disturbance, interspecies competition controls species richness. When species richness is increased due to a relaxation of competition, we also often observe an increase in species evenness, which can be defined as the similarity between population sizes of all species being compared. This is because as the dominant species become relatively less competitive, their populations tend to decline while the populations of other species tend to increase, leading to more similar (hence more 'even') population sizes across species. When evenness increases, if species richness stays the same or increases, we will also observe an increase in Shannon diversity. Thus when increasing disturbance relaxes interspecies competition, it allows more species to coexist. This may be reflected in several different indices, such as species richness, evenness, or diversity. Consequently, although these measures are formally distinct and can be statistically independent (Purvis and Hector 2000) because of their functional relationship they are often used interchangeably as measures of plant responses to disturbance. Thus here I will refer to

changes in richness and/or diversity of plants.

At high levels of disturbance, the biomass of individuals is cleared away or converted to detritus, reducing species diversity (i.e. potentially both richness and evenness). Thus disturbance refers to any process that relaxes competition at low levels (left side of hump) and degrades biomass at high levels (right side of hump), such as herbivory, fire, digging, etc. Notably, increases along the disturbance axis have been used to refer to increases in its frequency, elapsed time, extent, or duration (Shea et al. 2004). For the purposes of this paper I will refer to all such measures as different measures of disturbance intensity.

Other versions of the IDH interpret disturbance to mean environmental severity or stress, due to variation in abiotic factors such as nutrient or water availability (e.g., Michalet et al. 2006). Although related concepts, disturbance intensity and environmental severity or stress are not necessarily equivalent. This relates to the conceptual issue of whether disturbance is an endogenous or exogenous process (see below). Disturbance intensity generally conceptualizes disturbance as an endogenous process, i.e. carried out by some species in the community. Such processes result in patches of physical conditions, such as changes to soil texture, nutrient availability, or water accumulation, that are different from the conditions in areas that have not been disturbed. Environmental stress or severity conceptualizes the disturbance axis as driven by atmospheric or biogeochemical processes, or more generally by abiotic inputs to the ecosystem. 'Severity' would characterize the abiotic inputs, while 'stress' would describe the effect of those inputs on species. Environmental severity may result in changes in soil texture, nutrient availability or water accumulation, for example, equivalent to those caused by small mammal digging or herbivory. However, abiotic inputs causing environmental stress may show significantly different temporal, spatial, or feedback dynamics, and qualitatively and quantitatively different interactions with other ecological factors compared to small mammal disturbances. Using the concepts of environmental stress or severity rather than disturbance builds a

conceptual bridge between the IDH and studies of bottom-up control of food webs and trophic cascades (see Figure 1). Although stimulating, this link remains under-conceptualized.

A weakness of the IDH is that intermediate levels of disturbance (or stress) usually cannot be identified or defined *a priori* (Shea et al. 2004). Consequently, it is difficult to evaluate whether rising or falling (non-humped) diversity responses represent failures of the model or just the left or right sides of an incompletely measured hump (Waide et al. 1999, Mackey and Currie 2001).

What I will call the perturbation hypothesis (PH) is similar to the IDH but considers herbivory, as a trophic interaction, to be endogenous to community dynamics, unlike non-trophic disturbances (Proulx and Mazumder 1998). This thinking links disturbance via herbivory to models of trophic cascades and keystone predation (see Figure 1). 'Perturbation' is thus a term that signals the prioritization of trophic interactions when considering community dynamics, and which is used primarily by researchers with an interest in herbivory. In a meta-analysis, Proulx and Mazumder (1998) show that plant richness decreases with perturbation intensity in nutrient poor sites, while in nutrient rich sites plant richness increases. These results evoke the potential right and left sides of disturbance humps, but with the additional variable of nutrient availability modifying the species richness responses. Nutrient availability can be described as a measure of environmental stress. We should, however, note an incongruency: while in the IDH competition controls the response only on the left side of the hump (and is thus an implied variable not shown as its own axis in the graphical model) and disturbance that degrades biomass controls the right side, here nutrient availability controls the competition response on both sides of the hump.

It is not clear why the role of nutrient availability would be specific to 'endogenous' trophic effects. Other consumptions of plant biomass, such as fire (Bond and Keeley 2005), are usually considered exogenous processes. The responses of species in a given habitat may differ depending on whether the habitat is disturbed by fire or her-

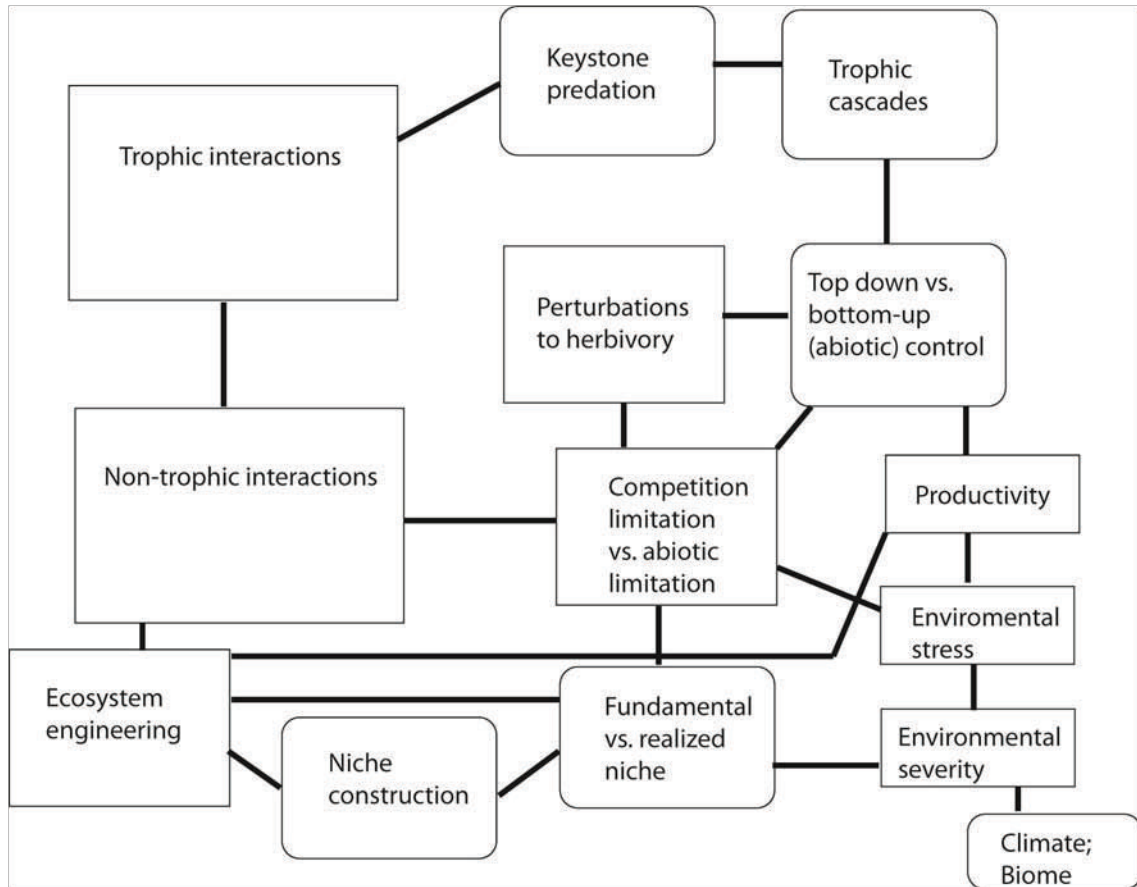


Figure 1. Relationships between key concepts in community ecology. Those shown in squares have been used to explain disturbance. Concepts in rounded squares are not directly implicated in disturbance ecology, but are conceptually linked and may have influenced terminology used in some studies of disturbance. The functional relationships between concepts, such as overlaps and nestedness, are not shown.

bivory (Bond and Keeley 2005). However, these differences are due to the evolutionary history of the adaptations to fire or herbivory present in the community, not to any fundamentally different endogenous and exogenous processes. Rather, at least for our purposes here, perturbations to herbivorous trophic interactions and non-trophic disturbances are all examples of disturbance regimes.

Finally, the ecosystem engineering hypothesis (EEH) as applied to small mammal disturbances (Wright and Jones 2004) predicts that small mammals can directly modify productivity (defined as the rate of conversion of abiotic inputs to biomass), including indirect measures such as soil nutrient availability. This may occur, for example, by species making changes to physical qualities of the soil or nutrient cycling rates. However, not all small mammal disturbances directly affect pro-

ductivity, limiting the model's scope. Unfortunately the model also provides no guidance as to the mechanisms or set of characteristics of disturbances that make them likely to directly affect productivity. Although such mechanisms and characteristics exist, lack of specificity in the model means that it is not well integrated with other research strands (see Figure 1). In the model, when small mammal disturbances move plant communities to intermediate levels of productivity, interspecies competition is relaxed and more species can coexist, as in the IDH. Unlike the IDH, but similarly to the PH, superior competitors emerge and dominate as productivity increases, such that competition controls the response on both sides of the hump (Wright and Jones 2004).

The modelled hump-shaped response in the EEH is valid only if we interpret productivity as a measure such as soil nutrient availability at a habi-

tat scale, for which such a unimodal species richness response may be observed (Waide et al. 1999). However, productivity also varies at a biogeographical scale across climate gradients and habitat types. This is because the rate of conversion of abiotic inputs to biomass in different parts of the world depends on both abiotic inputs, affected by climate and biogeochemical cycles, and by the physiology of plants present in the community, affected by their biogeographical distributions and evolutionary histories. The differences in productivity between, for example, deserts and tropical forests show a linearly increasing, not humped, relationship with species diversity or richness (Waide et al. 1999). The hump shaped response at habitat scales is a result of the species pools from which community compositions draw. In the absence of non-native species, species pools will be mainly adapted to average regional conditions, with only a few species, at the tail of the hump-shaped response, being well adapted to locally extreme or stressful conditions (Pärtel et al. 2007). Thus if disturbance increases productivity, this must be because it moved habitat conditions closer to those to which most species in the species pool are optimally adapted. The effects of any particular disturbance on species richness are thus contingent on the species pool.

The model

The Slope-Hump model incorporates four key variables and their interactions from the IDH, PH and EEH. The four variables are abiotic limitation, competition limitation, disturbance intensity and the response variable, species richness or diversity.

The concepts environmental stress / nutrient availability / productivity are reconceptualized as the first variable, which is abiotic limitation. The 'limitation' concept is based on the observation that factors may place limits on the population growth of a species, or delimit its realized niche (Dunson and Travis 1991). As the limitation is 'relaxed' the species escapes the constraint created by the limiting factors and its population expands. An equivalent way of stating this is that as abiotic inputs rise, productivity (the rate of conversion of abiotic inputs to biomass) can increase

and more biomass is produced. Plants can be either predominantly abiotically limited (e.g., temperature, nutrient or water limited) or competition limited, with variation in community composition, trophic structure, spatial heterogeneity, etc., potentially shifting the balance between the two (Grime 1973, LeBauer and Treseder 2008). Each species in a community may have different responses to a given set of abiotic conditions, and thus may be more or less abiotically limited under the same conditions. The second proposed variable is thus competition limitation. In deserts, local variations in productivity within the range typical for arid regions are always relatively more controlling than competition, and plant communities remain abiotically limited. At the other extreme, in tropical forests, for all levels of productivity associated with tropical conditions (which are absolutely higher than in deserts), competition determines plant species richness and communities are competition limited. Between the two extremes, both exert intermediate levels of limitation. Thus, although limitations are species-specific, for the purposes of the model by 'limitation' I mean the mean or range of limitations found in the species pool of a given community.

The Slope-Hump model thus proposes that the two key variables controlling the baseline conditions on which small mammal disturbances operate are abiotic and competition limitations (see Olofsson et al. 2002). Further, these variables are considered at two scales, the community scale and the biogeographic scale. Disturbance intensity, the third variable, demonstrates a hump-shaped relationship to plant species richness (or diversity), the response variable. In this model, disturbance is considered relative to the baseline competition and abiotic limitation conditions. The Slope-Hump model is shown using two different graphical visualizations of the model (Figures 2, 3). As can be seen from the figures, species richness is highest in arid habitats, declines as productivity increases along the climate/biogeographical habitat gradient, and at the other extreme of subtropical or tropical habitats, changes sign and becomes negative.

Comparison of models

The Slope-Hump model is an improvement over the IDH, PH and EEH models. Unlike these, it can predict the direction (negative or positive) of the disturbance effect on plant diversity or richness, as well as the relative magnitude of the effect. It does so by making the relationships between competition, productivity / nutrient availability / environmental stress, etcetera, disturbance, and richness graphically explicit through the use of the four key variables competition limitation, abiotic limitation, disturbance intensity and species richness. Like the IDH, it accounts for the effects of decomposition or removal of biomass (here, both sides of the hump), while more explicitly relating this to release of interspecific competition. This relationship is expressed through the disturbance-richness hump being represented as resting on, or relative to, the abiotic limitation/competition limitation slope. The model also takes into account both small community scale and large biogeographic scale variations in environmental stress or equivalently, the abiotic inputs to productivity, like versions of the IDH and the PH. By doing so, it also takes into account the contingent effects of species pools adapted to different local productivity conditions. Finally, as in the EEH, the disturbance humps explicitly move the plant community to different positions in productivity/competition space.

Model predictions

The model is applicable to all habitat types. Between arid and temperate regions, the increase in richness is predicted to get smaller, until it changes sign and becomes negative, roughly in subtropical or tropical habitats (Figures 2, 3). Since richness outcomes in the model are linear and continuous, I focus on predictions at the extremes of the model's range, i.e. arid and tropical conditions, with the expectation that readers can interpolate between the two. The Slope-Hump model predicts that for arid environment communities, disturbances that release the plant community from abiotic limitation should result in large, positive increases in plant species richness (Figures 2, 3). The magnitude of abiotic limitation depends on

productivity. In different regions, different inputs to productivity will be more limiting. Consequently, the magnitude of the disturbance effect will depend on which components of productivity are affected by the disturbance, and how sensitive the plant community is to changes in these. As an example, weather perturbations such as El Niño–La Niña cycles can dramatically increase precipitation, and should dramatically increase species diversity, given the available seed bank pool (Gutiérrez et al. 2010). Small mammal disturbances affecting soil nutrient availability should also have large positive effects, but may not reach the magnitude of effect produced by superabundant rainfall. By contrast, in tropical forests small mammal disturbances of an equal intensity would be predicted to reduce species diversity. The release from interspecific competition available from small mammal disturbances would not reduce competition significantly below the existing range. Moreover, small mammal disturbances may not liberate ecological niches over which competition is intense, for example patches with access to light. Only relatively catastrophic disturbances such as windfalls will reduce species competition for access to light, and even these may not affect plant diversity (Hubbell et al. 1999). Consequently, small mammal disturbances in highly productive biogeographical areas have the physical effects (decomposition or removal of biomass) common to all forms of disturbance, but no compensatory positive effect on the competition limitation of the plant community. This is the insight from the right hand side of the IDH hump. The predicted result is a local decrease in species diversity or richness.

Non-native species, or the overlap of two groups of species corresponding to different community types, can complicate this picture. For example, an invasive pioneer species in an old growth tropical forest may dominate competition for disturbed areas (Fujinuma and Harrison 2012). Note that while the contribution of non-native species to species richness remains small, their presence would not change the direction of the disturbance effect from negative to positive. Similarly, if disturbance facilitates the transition be-

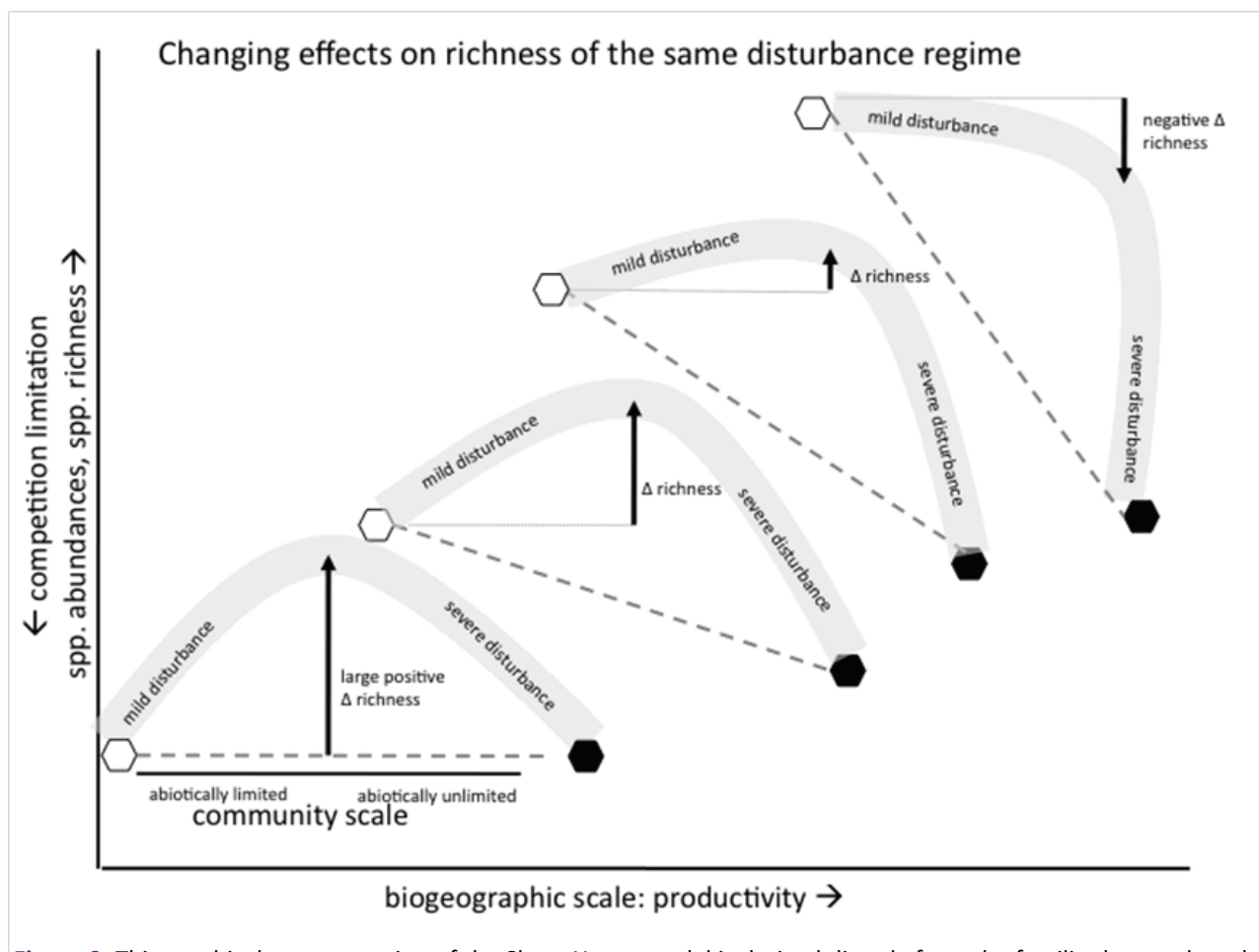


Figure 2. This graphical representation of the Slope-Hump model is derived directly from the familiar humped model of the Intermediate Disturbance Hypothesis. By collapsing four variables into two dimensions, the figure distorts certain details (compare Figure 3). On the other hand, this graphical representation is relatively intuitive. The dotted line shows a relationship between abiotic limitation (inset x-axis) and competition limitation in the absence of disturbance, with the two extreme tradeoffs shown as white and black hexagons. The disturbance regime is shown in grey. The change in richness under disturbance is shown as a black arrow. The four humps represent the same disturbance regime over four habitats across a biogeographic scale of increasing productivity, e.g., from a desert (left) to a tropical forest (right).

tween two community types, for example scrub and grassland, and the incoming community is species-poor compared to the original community, the disturbance regime appears to reduce species richness (Wesche et al. 2007, Wesche pers. comm.). Properly speaking, a given competition-abiotic limitation baseline and an associated disturbance hump in the Slope-Hump model only represents within-community changes in species richness, not community transitions. Where disturbances favor the establishment of keystone structure species that support a different plant community such transitions are likely to be observed.

The predictions for magnitude and direction of disturbance effects on plant species richness

made by the Slope-Hump model are qualitatively in agreement with current data from meta-analyses (Proulx and Mazumder 1998, Chase et al. 2000, Mackey and Currie 2001, Wright and Jones 2004, Root-Bernstein and Ebensperger 2012) and qualitative reviews (e.g., Olff and Ritchie 1998, Kerley et al. 2004) showing productivity- and competition-dependent humped responses that are strong and positive in more arid habitats, reduced in strength in less arid habitats, and null or negative in tropical, subtropical, and some temperate habitats. Nevertheless individual experiments may contradict the model. For example, Bakker et al. (2006) show that large herbivores slightly increased plant diversity in more-productive grassland/shrub/steppe habitats and slightly decreased

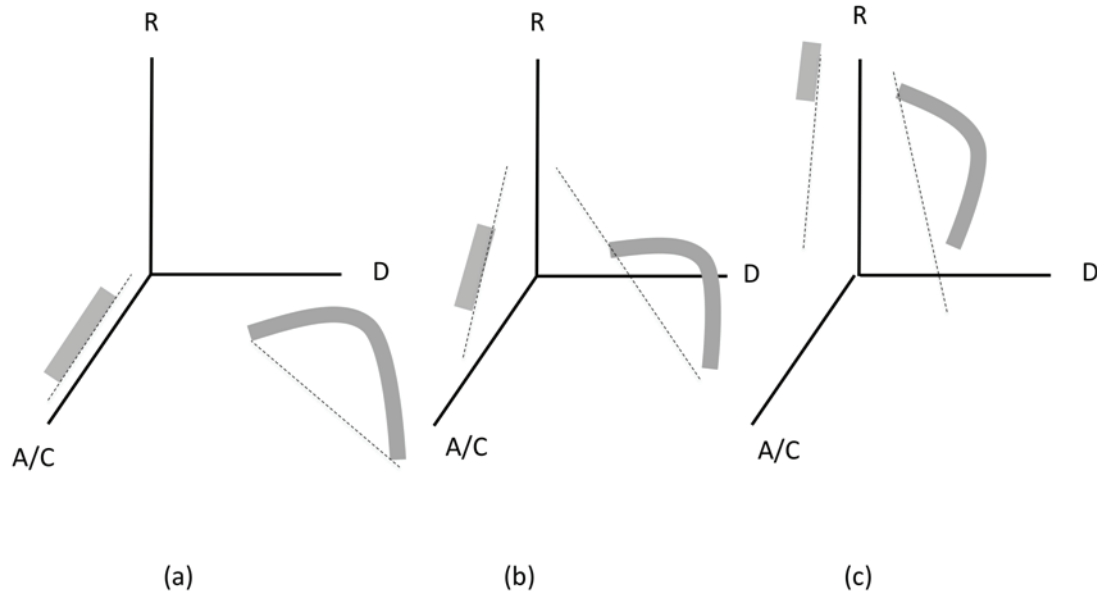


Figure 3. An alternative graphical representation of the Slope-Hump model. What this representation lacks in intuitiveness it makes up for in accuracy. A/C refers to a normalized relationship between abiotic and competition limitations. R is richness and D is disturbance. The slope and hump are represented as a discontinuous function, where the thick grey lines represent distributions of data points. The thin dotted lines show paired equal slopes which can be thought of as lines along a cone's surface that both the slope and the hump stand on. From (a) to (b) we move from a desert to a temperate habitat, and from (b) to (c) we move from a temperate habitat to a tropical forest.

it in less-productive ones, while small herbivores had no effect. Since these habitats are moderately productive at a biogeographic scale, these disturbance effects could be due to measuring richness at different positions along similar disturbance regime humps (Figure 3b). However, evaluating why or whether these results contradict the model is difficult because the types and intensities of disturbance differed across sites of differing productivity (Bakker et al. 2006). Quantitatively testing the model remains challenging due to the multiple measures commonly used for productivity, competition, and disturbance (Goldberg et al. 1999, Waide et al. 1999, compare Rogers et al. 2001, Wesche et al. 2007, Galvez Bravo et al. 2009). Small mammal disturbances can also directly or indirectly affect the species diversity of bacteria, invertebrates, birds, reptiles, amphibians, and other mammals (Root-Bernstein and Ebensperger 2012). Common measures of productivity and competition do not always clearly apply to such communities, and the effects of disturbance on non-producers in the food web may be due to other mechanisms, making the Slope-Hump model potentially inapplicable to them.

The Slope-Hump model should be useful for designing plant community restoration or conservation interventions, using small mammals or artificial small-mammal-like disturbances (Dhillon 1999). For example, in a productivity limited plant community, disturbances that accumulate nutrients or water, such as small pits, should be preferred. In a competition limited plant community dominated by a few species, conservationists should choose a form of disturbance that removes biomass of the dominant competitor, for example herbivory-like cropping, or small mounds or run-way-like features (for the effects of different forms of disturbance see Root-Bernstein and Ebensperger 2012). If the region is affected by significant productivity gradients or variations (e.g., El Niño–La Niña cycles, fertilizer), disturbance intensity would need to be higher for higher productivity in order to observe a similar magnitude of effect on species richness. In temperate or subtropical regions, increases in productivity could also shift a system to a position in competition limitation / abiotic limitation space (rightwards along the graph) where the disturbance regime becomes ineffective or changes sign

to have negative effects. Disturbances could also be used along with nutrient-stripping approaches to restoration (Prober and Wiehl 2012) in order to maximize the diversity of native plants tolerating a lower nutrient level than invasive species.

I end with two specific predictions. First, there are many Southern Hemisphere small mammals and marsupials whose disturbance effects on plant diversity are understudied or unknown. One example is *Cavia aperea*, a semi-fossorial group-living runway-making cavie or guinea pig with a distribution stretching from the semi-arid grasslands of northern Argentina to the tropical border of the Amazonian rainforest. The Slope-Hump model predicts that for equivalent *C. aperea* disturbance regimes (e.g., equal runway densities), the plant diversity response should switch from strong and positive to null to negative, moving northwards. Second, long term data sets that include measures of small mammal disturbance, as well as measures of competition and productivity (if these exist), should find that their data over time, as disturbance, competition and productivity shift, form a slope and hump as shown in Figure 3. Disturbed and undisturbed systems should show historicity affecting the magnitude of diversity changes under invasive plant arrival or restoration. Importantly, to evaluate the model predictions, disturbance intensity and not just small mammal presence, as well as competition and abiotic limitation must all be measured across conditions.

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