

# Disturbance and change in biodiversity

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Understanding how disturbance affects biodiversity is important for both fundamental and applied reasons. Here, I investigate how disturbances with different ecological effects change biodiversity metrics. I define three main types of disturbance effects: *D* disturbance (shifts in mortality rate), *B* disturbance (shifts in reproductive rates) and *K* disturbance (shifts in carrying capacity). Numerous composite disturbances can be defined including any combination of these three types of ecological effects. The consequences of *D*, *B* and *K* disturbances, as well as of composite *DBK* disturbances are examined by comparing metrics before and after a disturbance, in disturbed and undisturbed communities. I use simulations of neutral communities and examine species richness, total abundance and species abundance distributions. The patterns of change in biodiversity metrics are consistent among different types of disturbance. *K* disturbance has the most severe effects, followed by *D* disturbance, and *B* disturbance has nearly negligible effects. Consequences of composite *DBK* disturbances are more complex than any of the three types of disturbance, with unimodal relationships along a disturbance gradient arising when *D*, *B* and *K* are negatively correlated. Importantly, regardless of disturbance type, community isolation enhances the negative consequences and hinders the positive effects of disturbances.

**Keywords:** perturbation; species richness; neutral model; stress; threat; diversity

## 1. INTRODUCTION

The role of disturbance in shaping biodiversity is widely recognized. Effects of disturbance on biodiversity have been studied in a great variety of ecosystems ranging from tundra communities (Jorgenson *et al.* 2010) to coral reefs (Graham *et al.* 2009), a range of organisms extending from bacteria (Binh *et al.* 2007) to primates (Bicknell & Peres 2010) and at multiple levels of organization including molecular pathways (Spagnuolo *et al.* 2009) and ecosystem functioning (Hotes *et al.* 2010). The types of disturbance involved include everything from single tree-falls (Brokaw 1985) to ecological catastrophes (Hughes 1994). A search in web-of-science with keywords *diversity* and *disturbance* finds over 6500 publications. This large body of literature is largely fuelled by the need to quantify effects of disturbance (typically of anthropogenic nature) on communities, in order to guide conservation efforts and the management of ecological resources. Developing general guidelines to predict when and how biodiversity patterns should change following a disturbance is a crucial matter for this purpose.

From a historical perspective, disturbance has long been present in ecological theory. Early views focused on succession, which took communities from the colonization of barren space by pioneer species, to highly complex and diverse climax communities

(Clements 1916). The importance of disturbance in this context is that it leads to secondary succession and sometimes prevents communities from reaching their climax state. The progressive realization of the roles of grazing and predation on delaying competitive exclusion led to the formulation of the intermediate disturbance hypothesis (Grime 1973; Connell 1978). This hypothesis proposes that species richness should be maximized under intermediate levels of disturbance because at low levels of disturbance superior competitor species monopolize resources and exclude other species, whereas at high disturbance levels only the most resistant species survive. This unimodal relationship between species richness and disturbance has become an ecological paradigm (Wilkinson 1999). Numerous studies have empirically validated this hypothesis, however, a meta-analysis revealed that conflicting and non significant patterns are common (Mackey & Currie 2001). These inconsistent results may be partly driven by the variety of events that are included under the umbrella of disturbance, and their differences in ecological consequences. Therefore, in this paper, I compare effects of different ecological disturbances for biodiversity (see below under definition of disturbance).

Disturbance has since become a prevalent feature in ecological theory. A complete review of disturbance in ecological theory is beyond the scope of this paper, but some examples include: patch dynamics models (Shugart & Seagle 1985; White & Pickett 1985), fluctuation-mediated coexistence (Chesson & Warner 1981) and life-history trade-offs (Tilman 1994). More recently, neutral models (*sensu* Bell 2000;

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Hubbell 2001) have also begun to be used to assess the ecological effects of disturbance. For example, a spatially explicit neutral model has shown that disturbance increases time to extinction and can delay (or prevent) mono-dominance (Gardner & Engelhardt 2008). Empirical support for neutral models as general explanations for biodiversity patterns has been controversial, with even the same datasets reported as evidence for and against them (McGill 2003; Volkov *et al.* 2003, 2007; Dornelas *et al.* 2006). However, neutral models are valuable tools for understanding ecological dynamics, and a lot can be learnt from deviations between observed and predicted patterns (Alonso *et al.* 2006). In fact, differences among communities in terms of disturbance history have been invoked to explain discrepancies between observed patterns and neutral model predictions (Dornelas *et al.* 2006). Incorporating disturbance seems to improve neutral model fits to experimental data (Benedetti-Cecchi *et al.* 2008). Moreover, neutral models have been used to explore the relationships between productivity and species richness, and between disturbance and species richness (Kadmon & Benjamini 2006).

Here, I build on this approach to explore how different ecological effects of disturbance change biodiversity patterns. I start by developing a definition of disturbance, which leads to a classification of disturbances according to their ecological effects. Then I use neutral model simulations to explore effects of these different types of disturbances on community structure. I focus on immediate effects of disturbance and, in line with the theme of temporal aspects of biodiversity patterns (Magurran & Dornelas 2010) and with a prevalent approach in empirical studies (Eberhardt 1976), I compare communities before and after a single disturbance event. Finally, I discuss how estimating the three main ecological effects of a disturbance may help predict its consequences for the community.

#### (a) *Definition of disturbance*

The word disturbance is used in ecology to refer to a great variety of phenomena. Examples of disturbance include fires, storms, diseases, volcanic eruptions, earthquakes, contaminant spills, land clearing and dredging among many others (see Dornelas *et al.* 2010 for an overview of sources and characteristics of disturbance). Therefore, it is not surprising that definitions of disturbance are wide and inclusive. In this section, I focus on the fundamental characteristics that make an event an ecological disturbance, develop a definition of disturbance based on its ecological consequences, and highlight three main types of ecological effects of disturbances.

One fundamental characteristic of disturbance is its discrete nature in time and space (White & Pickett 1985). Disturbance is temporary and localized, and therefore is not to be confounded with stress, which may also change ecological communities but in more permanent and diffuse ways. This distinction is akin to pulse and press perturbations in experimental ecology (Bender *et al.* 1984). So for example,

climate change may be a stress to biodiversity, but its global and permanent nature mean that it is not a disturbance. Storms, on the other hand, which are predicted to increase under climate change (Schiermeier 2005), are potential sources of disturbance.

The word disturbance is often used to refer to causes of disturbances. In contrast, here I focus on the actual changes that occur regardless of their source, as these are what is most relevant from a theoretical ecology perspective. In this respect, increased mortality is commonly referred to as an essential effect of disturbance. In fact, one definition of disturbance is that these are events that cause mortality, displacement or damage individuals (Sousa 1984). Sub-lethal effects are also mentioned: disturbances have been defined as events that kill or cause loss of biomass (Huston 1994). This means that there is a negative connotation to the word disturbance, which can be interpreted from a theoretical perspective as a negative shift in demographic rates (i.e. increased mortality and/or decreased growth and reproduction). However, a common consequence of disturbance is the release of resources, previously trapped in living organisms (White & Pickett 1985). Resource pulses resulting from disturbance may consequently enhance survival or reproductive rates, and/or increase the number of individuals a community can accommodate (Holt 2008). Therefore, disturbance can cause both positive and negative shifts in demographic parameters.

Ecological disturbance can, thus, be defined as an event that causes temporary and localized shifts in demographic rates. Specifically, there are three principal ways in which disturbance can affect community dynamics: by changing mortality rates (henceforth *D* disturbance), birth rates (*B* disturbance) or carrying capacity (*K* disturbance). Often, a disturbance will affect more than one of these parameters, and we can refer to these disturbances by combining the corresponding letters (e.g. *DBK* disturbance when all three parameters are involved). The question that arises is whether these different types of disturbance have similar consequences in terms of biodiversity patterns. To answer this question, I incorporate these different types of disturbance into neutral models and explore their consequences using multiple biodiversity metrics.

#### (b) *Which biodiversity patterns?*

There are literally hundreds of metrics of community structure designed with the purpose of detecting effects of disturbance on biodiversity (see Dornelas *et al.* 2010 for a review). Most studies focus primarily on species richness, which is a fundamental metric because it summarizes extinctions and colonizations. However, species richness can be a relatively insensitive metric because it does not reflect shifts in relative abundance, which precede extinctions and can have dramatic consequences for ecosystem functioning (Gaston & Fuller 2008). Therefore, two other metrics of community structure are used: total abundance and species abundance distributions (SADs), which have recently been subject to renewed

interest (McGill *et al.* 2007) and whose potential as ecological indicators is re-emerging (Dornelas *et al.* 2009). These metrics are sufficiently general, because they do not depend on species identities, and therefore can be used to compare communities in different ecosystems, or different biogeographic regions.

These metrics reflect important community characteristics and measure facets of biodiversity that are complementary to species richness. Total abundance is a metric of productivity and community capacity, a fundamental attribute of the community in terms of ecosystem processes. Reports of unimodal productivity–diversity relationships (Tilman *et al.* 1997) in combination with the intermediate disturbance hypothesis (Grime 1973; Connell 1978) lead to the hypothesis that productivity has a unimodal distribution with disturbance. SADs combine information about the number of species, their total and relative abundances. SADs have been shown to change with disturbance and proposed as diagnostic tools for effects of pollution and landscape alteration (Gray 1981, 1983; Uglund *et al.* 2007; Dornelas *et al.* 2009). Specifically, the modal class of SADs is predicted to shift to the left with disturbance, as rare and moderately abundant species become rarer.

## 2. METHODS

### (a) Model description

The model is a modified version of the models used by Bell (2000) and modified by Kadmon & Benjamini (2006). It focuses on the dynamics of a local community with a carrying capacity of  $\mathcal{J}$  individuals, undergoing deaths with a *per capita* probability  $d$ , and births with *per capita* probability  $b$ , which are equal for all species. Each individual site in the local community receives immigrants with probability  $m$ , from a regional species pool with  $S$  species. SAD at the regional scale follows a Poisson lognormal distribution with parameters  $\sigma$  and  $\mu$ . As in Kadmon & Benjamini's model (2006), the total abundance of the local community at each time step is the result of an equilibrium between births, deaths and immigrations, rather than a fixed number and is denoted as  $\mathcal{J}_t$ . Therefore, this model applies to both saturated and unsaturated communities, and total abundance in itself becomes a model prediction of community productivity. The three types of disturbance are introduced as modifiers of the mortality rate  $d$  (as  $D*d$ ), the birth rate  $b$  (as  $B*b$ ), and the carrying capacity  $\mathcal{J}$  (as  $K*\mathcal{J}$ ). Recruits compete for vacant spots whenever the number of recruits exceeds the number of empty spots, which are limited by carrying capacity ( $\mathcal{J}$ ). Pseudo code for the model is presented in figure 1 (R code can be obtained from the author).

The model is a stochastic individual-based simulation. On average, dynamics of species  $i$  are expected to follow these expressions:

$$\text{if } \mathcal{J}_t > K\mathcal{J},$$

$$N_i^{t+1} = N_i^t \left( 1 - Dd - \frac{\mathcal{J}_t(1 - Dd) - K\mathcal{J}}{\mathcal{J}_t} \right), \quad (2.1)$$

where  $N_i^t$  is the abundance of species  $i$  in the local community at time  $t$ . Otherwise, if  $\mathcal{J}_t + (Bb - Dd)\mathcal{J}_t + m\mathcal{J} > K\mathcal{J}$

$$N_i^{t+1} = N_i^t(1 - Dd) + (BbN_i^t + mN_i^R) \times \frac{K\mathcal{J} - \mathcal{J}_t(1 + Dd)}{K\mathcal{J}}, \quad (2.2)$$

where  $N_i^R$  is the abundance of species  $i$  in the regional species pool, and is constant. Otherwise,

$$N_i^{t+1} = N_i^t(1 - Dd + Bb) + mN_i^R. \quad (2.3)$$

### (b) Simulations

The number of replicate simulations needed to obtain stable predictions with this model was estimated by running 1000 replicate simulations for a subset of four parameter combinations:  $S$  of 50 and  $500 \times m$  of 0.01 and 0.9. Each replicate simulation corresponded to a realization of the Poisson lognormal regional source of immigrants. These simulations were ran for 10 000 time steps and with  $\mathcal{J}$  equal to 1000 and  $d$  and  $b$  equal to 0.05. Comparison of SADs, species richness and total abundance revealed that 100 replicates sufficed to obtain stable predictions, so this was the number used in subsequent analysis. Model predictions presented correspond to an arithmetic mean of the biodiversity metrics calculated for each of the 100 replicate simulations.

The effects of disturbance on biodiversity patterns were measured by comparing communities before and immediately after a disturbance event (which lasted a single time step). Community dynamics were run for 10 000 time steps (500 turnovers of the community) without disturbance (i.e. with  $D = B = K = 1$ ) for the following 18 parameter combinations:  $\mathcal{J}$  of 1000, 10 000 and 100 000,  $S$  of 50 and 500 and  $m$  of 0.01, 0.1 and 0.5. These simulations established the pre-disturbance picture, which was characterized in terms of species richness (number of species with abundance greater than zero in the focal local community), total abundance (sum of abundances of all species in the local community) and SAD (plotted as a Preston plot). At time step 10 001, disturbance was introduced by running the simulation for one time step with demographic rates multiplied by the parameters  $D$ ,  $B$  and  $K$ . The short duration of the disturbance events is justified by the definition of disturbance followed here, and the aim of exploring immediate effects of disturbances on the community. This model can also be used to explore the effects of different disturbance regimes on longer-term species coexistence, but this is beyond the scope of this paper. Running simulations with varying values for the disturbance parameters created a disturbance gradient, which included both positive and negative disturbances, as well as a no disturbance control (i.e. with disturbance parameters equal to 1). For  $D$  disturbances,  $D$  varied from 0.0312 to 16 (in a log 2 scale), while  $B$  and  $K$  were equal to 1. These values correspond to a minimum total mortality rate of 0.001, or a single individual dying in the smallest

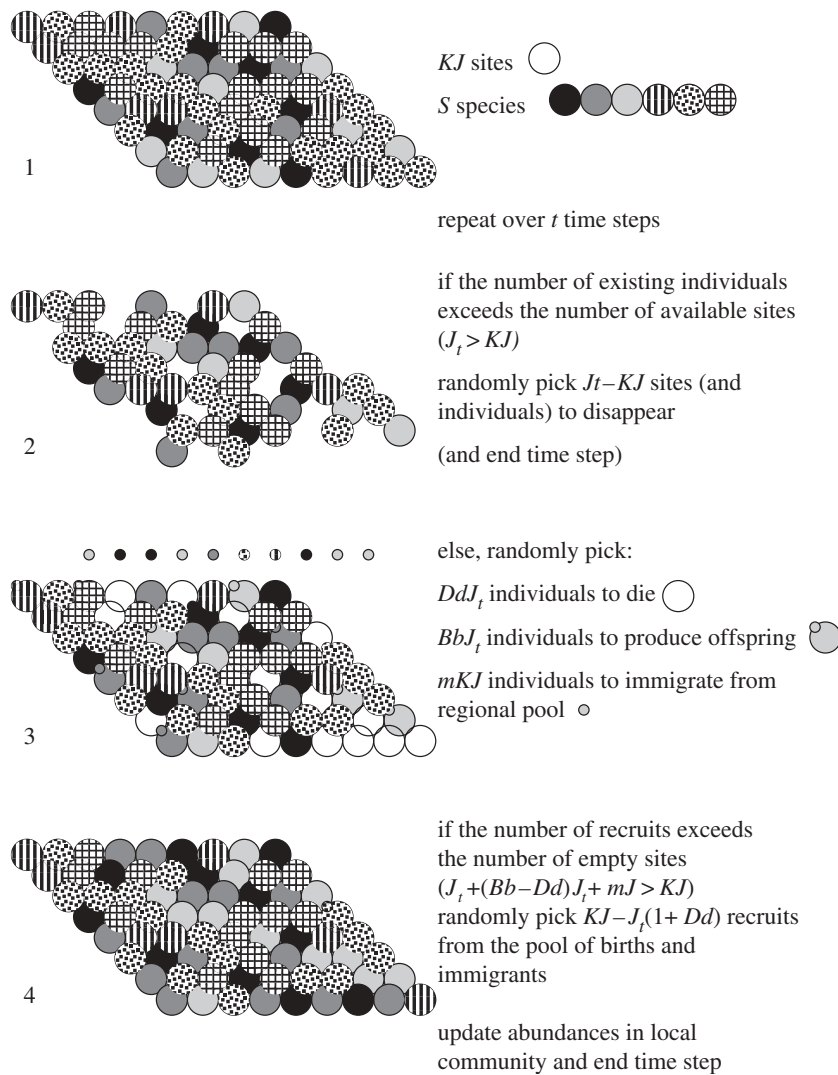


Figure 1. Model dynamics: pseudo-code used for the simulations (R code can be obtained from the author). Baseline simulations were ran 10 000 time steps (with disturbance parameters  $D$ ,  $B$  and  $K$  set to 1) after which communities were disturbed, with disturbance events lasting 1 time step.

communities, and a maximum total mortality rate of 0.8.  $D < 1$  corresponds to a decrease in mortality (i.e. a positive disturbance), and  $D > 1$  to an increase in mortality (i.e. a negative disturbance). For  $B$  disturbances  $B$  varied from 0 to 2 (intervals of 0.2), while  $D$  and  $K$  were equal to 1. These values correspond to a minimum total birth rate of 0 (total reproductive failure), and a maximum total birth rate of 0.1.  $B < 1$  corresponds to a decrease in fecundity (i.e. a negative disturbance), and  $B > 1$  to an increase in fecundity (i.e. a positive disturbance). For  $K$  disturbances  $K$  varied from 0.2 to 2 (intervals of 0.2), while  $D$  and  $B$  were equal to 1. These values correspond to proportional changes in total carrying capacity:  $K < 1$  corresponds to a decrease in carrying capacity (i.e. a negative disturbance), and  $K > 1$  to an increase in carrying capacity (i.e. a positive disturbance). These parameter values were selected to include extreme scenarios and after preliminary simulations showed that they encompassed both saturated and unsaturated communities. Two additional disturbance types were explored which included combinations of  $D$ ,  $B$  and  $K$ : in  $DBKu$  the three parameters varied in unison from positive to negative across the values

used in the single disturbance events; in  $DBKr$ ,  $K$  was negatively correlated with  $D$  and  $B$  to explore the ‘realistic’ scenario of increased resource availability following a mass mortality. The post-disturbance scenario was then characterized for each disturbance type similarly to the pre-disturbance scenario.

### 3. RESULTS

Effects of disturbance were modulated by immigration rate ( $m$ ), but not affected by community size ( $\mathcal{J}$ ) and regional species richness ( $S$ ). Therefore only results of two parameter combinations ( $\mathcal{J}=10\,000$ ,  $S=150$ ,  $m=0.01$  and 0.5) are reported. In general, isolated communities were more severely affected by negative disturbance and benefited less from positive disturbance.

Disturbance effects on species richness were parallel but more pronounced on total abundance (figure 2). The two metrics increased or were unaffected by positive disturbance and decreased with negative disturbance, but the size of the effect varied with disturbance type. While positive  $D$  disturbance had no effect on any of the metrics, negative  $D$  disturbance



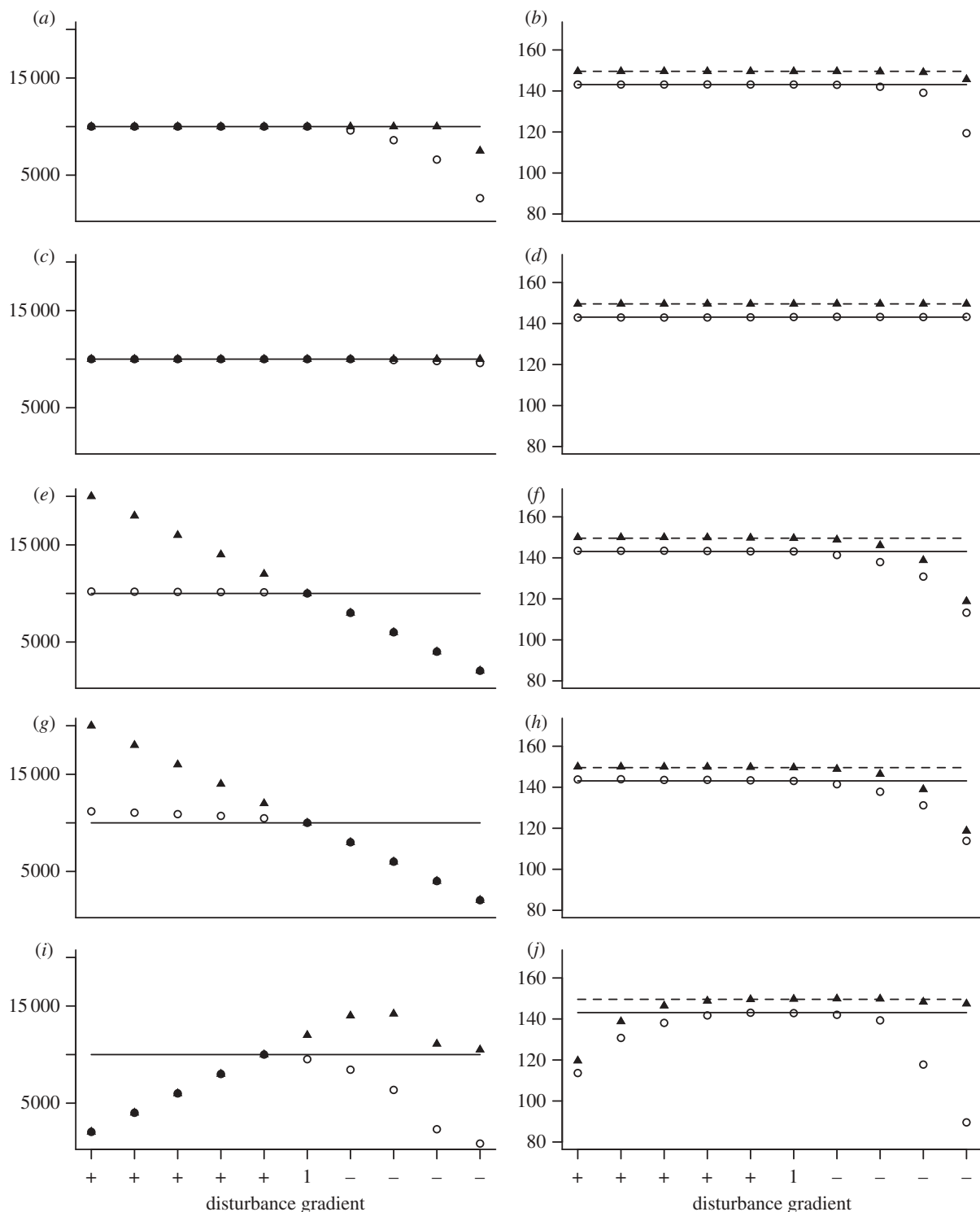


Figure 2. Changes in total abundance and species richness across gradients of different types of disturbance: line shows the before disturbance values (solid line for  $m = 0.01$  and dashed line for  $m = 0.5$ ), and disturbance gradient goes from severe positive to severe negative from left to right on the  $x$ -axis; unfilled circles represent mean of 100 simulated communities with  $m = 0.01$ , and filled triangles  $m = 0.5$ ; (a,c,e,g,i) report total abundance and (b,d,f,h,j) report species richness; (a,b)  $D$  disturbances, (c,d)  $B$  disturbances, (e,f)  $K$  disturbances, (g,h)  $DBKu$  disturbances, and (i,j)  $DBKr$  disturbances. Model parameters are  $\mathcal{J}$  of 10 000,  $S$  of 150.

decreased both metrics (but only in the most severe intensity in the case of high immigration communities). In terms of  $B$  disturbance, they produced no effect whatsoever on the two metrics. Positive  $K$  disturbance, on the other hand, increased total abundance (albeit only marginally in the case of isolated communities), but had a negligible effect on

species richness. Negative  $K$  disturbance decreased both metrics more severely than  $D$  disturbance. The effects of negative  $DBKu$  disturbance followed those of  $K$  disturbance closely, except positive  $DBKu$  disturbance generated a stronger increase than  $K$  disturbance for both metrics in isolated communities.  $DBKr$  disturbance created a unimodal effect on all

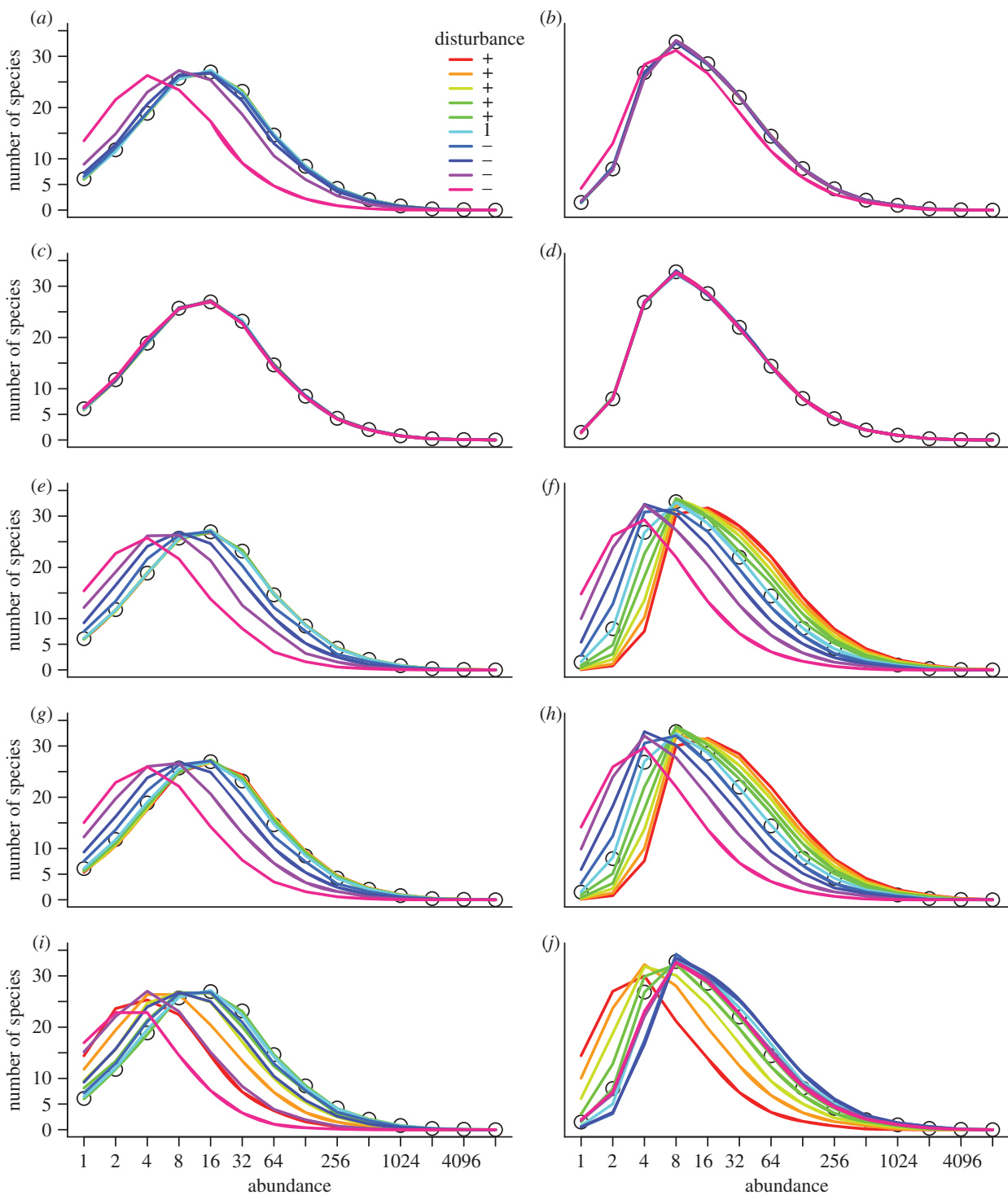


Figure 3. Changes in species abundance distributions caused by gradients of different types of disturbance: circles mark before disturbance values, and lines after disturbance. (a,b) *D* disturbance, (c,d) *B* disturbance, (e,f) *K* disturbance, (g,h) *DBKu* disturbance, and (i,j) *DBKr* disturbance. Model parameters are  $\mathcal{J}$  of 10 000,  $S$  of 150 and  $m$  of 0.01 for (a,c,e,g,i) and 0.5 for (b,d,f,h,j).

metrics, as both negative *K* with positive *D* and *B*, and positive *K* with negative *D* and *B* decreased species richness and total abundance in isolated communities. However, up to a threshold the latter lead to an increase in total abundance in high immigration communities.

Effects of different types of disturbance on SADs were consistent but varied in intensity with immigration rate (figure 3). Positive disturbance shifted the SADs to the right (all species became more abundant),

whereas negative disturbance shifted the SADs to the left (all species became less abundant). Positive *D* disturbance had no effect on SADs, and the effects of negative *D* disturbance were only evident for the most severe intensity in high immigration communities. *B* disturbance had no visible effects on SADs. Negative *K* disturbance shifted SADs to the left, but shifts to the right with positive *K* disturbance were only observed in high immigration communities. Effects of *DPKu* disturbance were indistinguishable

from those of  $K$  disturbance.  $DPK_r$  disturbance leads to shifts to the left in SADs.

#### 4. DISCUSSION

Changes to biodiversity patterns mediated by disturbance were qualitatively similar for the  $D$  and  $K$  disturbance types.  $B$  disturbance was the exception, with no effects apparent, even in the most severe case (local reproduction was completely suspended). This result is driven by the fact that in this model death is the engine of change: unless more individuals die, there is no scope for change in the community. Different results are expected in the case of non-overlapping generations, where the entire community is constantly replaced, and reproductive failure in one time step can compromise the survival of the entire community.

More often than not, disturbance involves shifts in more than one demographic parameter. Hence, from a practical perspective, the composite disturbances  $DBK_u$  and  $DBK_r$  are the most interesting scenarios explored here. When  $D$ ,  $B$  and  $K$  vary in the same direction, carrying capacity ( $K$ ) is the overwhelming driver of change. This makes intuitive sense, as reduced carrying capacity affects communities more deeply than both mortality and fecundity by hindering recovery. Even if there are potential recruits following a disturbance, there is no recovery if community capacity is reduced. Hence, disturbances that affect carrying capacity are expected to have the most drastic and lasting consequences.

When  $D$ ,  $B$  and  $K$  are negatively correlated, the patterns become more complex and trade-offs occur. Despite increased mortality and failed reproduction, increased carrying capacity can increase total abundance, and prevent species richness loss. Moreover, this is the only type of disturbance where a unimodal pattern in the biodiversity metrics was observed along the disturbance gradient, as predicted by the intermediate disturbance hypothesis (Grime 1973; Connell 1978). It must be noted that all post-disturbance communities had species richness values lower or equal to the pre-disturbance values, and species richness was highest for the lowest intensity disturbances. This may be due to  $D$  and  $B$  being positively correlated in the scenarios explored. Kadmon & Benjamini (2006) show, using a similar model, that the shape of species-richness–disturbance ( $D$ ) relationships varies from positive, to unimodal and then negative depending on the level of productivity ( $B$ ) and vice versa. Hence, intermediate-disturbance effects arise even in the absence of species differences in competitive ability and life-history traits, as long as there are community-wide negative correlations in  $D$ ,  $B$  and  $K$  along the disturbance gradient.

The parallel responses of all the biodiversity metrics used in this study suggest that, in agreement with the more individuals hypothesis (Srivastava & Lawton 1998), changes observed are largely driven by total community abundance. According to this hypothesis, higher total abundances allow larger population sizes, which minimize stochastic extinctions, and

thus maximize species richness. A comparison between panels in figure 2 suggests that total abundance and species richness vary in a similar way, but the latter also seems to be limited by immigration and regional species richness.

Community isolation plays an important role in modulating effects of disturbances. Isolated communities are more severely affected by negative disturbances because there are no immigrants to buffer the impact of enhanced mortality and reduced local reproduction. Additionally, isolated communities are less affected by positive disturbances because fewer immigrants take advantage of beneficial conditions and colonize available resources. This pattern is linked to the dilution effect (Kadmon & Benjamini 2006) according to which the ratio between local births and immigrants influences the number of species that coexist in the disturbed community. This result is important from the point of view of management and conservation, as it lends theoretical support to the widely recognized importance of maintaining connectivity among communities (Saunders *et al.* 1991).

In combination, these results show how identifying (even if only qualitatively) how  $D$ ,  $B$  and  $K$  are affected by a disturbance can help predict if and how biodiversity patterns are expected to change. For example, we can now predict that changes to carrying capacity in isolated communities are expected to have the most severe effects on biodiversity. We can also predict that consequences even of severe disturbance may be negligible if, for example, increased mortality rates are accompanied by an increase in available resources (and hence carrying capacity) and there are available recruits. Although, these predictions make intuitive sense, the modelling framework developed here allows quantifying how much each demographic parameter needs to change in order to create an effect of a certain magnitude.

In summary, the results of this study suggest that it is possible to predict general effects of disturbance on the biodiversity metrics explored here. If we can predict how a disturbance affects demographic rates of the community ( $D$ ,  $B$  and  $K$ ) the approach explored here suggests that we can generate theoretical predictions for how SADs, total abundance and species richness are expected to change. This sort of prediction is easily extended to other biodiversity metrics. This generates quantitative theoretical predictions against which empirical patterns can be compared. To obtain these predictions we must focus on questions more specific than whether a disturbance affects biodiversity. Specifically, we need to ask how disturbance affects community mortality rates, reproductive rates and carrying capacity. In the words of May (1988) ‘*We do not end up with a list of answers, but rather a list of more sharply focused questions*’.

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