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REVIEW AND SYNTHESIS

Reciprocal relationships and potential feedbacks between biodiversity and disturbance

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Abstract

Two major foci of ecological research involve reciprocal views of the relationship between biodiversity and disturbance: disturbance determines community diversity or diversity determines realized disturbance severity. Here, we present an initial attempt to synthesize these two approaches in order to understand whether feedbacks occur, and what their effects on patterns of diversity might be. Our review of published experiments shows that (i) disturbance severity can be both a cause and a consequence of local diversity in a wide range of ecosystems and (ii) shapes of the unidirectional relationships between diversity and disturbance can be quite variable. To explore how feedbacks between diversity and disturbance might operate to alter expected patterns of diversity in nature, we develop and then evaluate a conceptual model that decomposes the relationships into component parts, considering sequentially the effect of diversity on disturbance severity, and the effect of realized disturbance on diversity loss, subsequent recruitment, and competitive exclusion. Our model suggests that feedbacks can increase mean values of richness, decrease variability, and alter the patterns of correlation between diversity and disturbance in nature. We close by offering ideas for future research to help fill gaps in our understanding of reciprocal relationships among ecological variables like diversity and disturbance.

Keywords

Biodiversity, disturbance, ecosystem function, feedback, intermediate disturbance hypothesis, stability.

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INTRODUCTION

Interactions among ecological entities – be they individuals, populations or species – are almost always reciprocal, but each unidirectional effect is most often studied as an independent phenomenon (Agrawal *et al.* 2007). For example, ecological studies of mutualism often focus on the effect of host on guest or vice versa, rather than examining both simultaneously (Cushman & Beattie 1991). Studies that do include reciprocal effects illustrate that explicit and simultaneous examination of both directional effects often leads to different conclusions about mean states or dynamics than consideration of either unidirectional effect alone. For instance, at the population or species level, feedbacks between predator and prey or between mutualists have important implications for both ecological and evolutionary dynamics that are not necessarily predictable from only one direction of causation (Cushman & Beattie 1991; Thompson & Pellmyr 1992; Krebs *et al.* 1995; Yoshida *et al.* 2003). Reciprocal relationships can also occur at the community level. For example, it is broadly appreciated that variation in diversity can be both a cause and a consequence of variation in community productivity (Loreau *et al.* 2001; Chase & Leibold 2002; Schmid 2002; Contardo Jara *et al.* 2006) or resource density (Cardinale *et al.* 2006), though few studies consider both directions of causation simultaneously (Agrawal *et al.* 2007). Feedbacks might thus occur among these, or other community-level processes, but empirical investigations are scarce. Here, we consider the potential consequences of feedbacks between diversity and disturbance as a model for incorporating feedbacks into community-level processes more broadly.

A major focus of ecological research is to understand how community properties contribute to the maintenance of biodiversity (Pianka 1966; Connell 1978; Huston 1979). For example, research on how non-equilibrium forces (e.g. disturbance) help to maintain species diversity has generated a widely accepted paradigm, the intermediate disturbance hypothesis (IDH). The IDH predicts that intermediate frequencies or intensities of disturbance maximize diversity of sessile, space-holding species (e.g. trees, corals) because lower disturbance levels enable competitively dominant species to monopolize resources and decrease diversity, whereas higher disturbance levels enable only colonizing species to establish (Connell 1978; Sousa 2001). Numerous studies have documented an IDH pattern (Mackey & Currie 2001; Shea *et al.* 2004) but the relationship is far from universal (Mackey & Currie 2001), suggesting that other factors also influence how disturbance impacts diversity. For example, monotonic increases in diversity with decreasing disturbance can be attributed to increased habitat complexity at low disturbance (Bruno *et al.* 2003). In addition, the relationship between diversity and disturbance may be dependent on the level of productivity (Huston 1979).

A largely separate body of ecological research has examined how biodiversity affects community or ecosystem properties such as productivity and nutrient cycling (i.e. biodiversity–ecosystem function; Loreau *et al.* 2002). Included in this body of work is the long-standing debate on the relationship between diversity and community stability (MacArthur 1955; May 1973; Tilman 1999; McCann 2000). Although stability can be defined in many different ways (see, e.g. Pimm 1984), experimental explorations of the diversity–stability relationship often focus on the effect of diversity on community response to specific disturbance events, revealing several sound theoretical and biological mechanisms by which diversity might influence the magnitude of loss to (resistance) or rate of recovery from (resilience) disturbance. For example, diversity can enhance the probability of including resistant species that can compensate for the loss of vulnerable species (i.e. the insurance hypothesis; e.g. Tilman 1996). In addition, diversity is often associated with increased phenotypic breadth of morphology or physiology; this variation can enhance the response to some disturbances via complementarity or facilitation (e.g. Mulder *et al.* 2001), but it can also increase susceptibility to other forms of disturbance (e.g. Allison 2004). Thus, although physical forces that generate a disturbance are unlikely to be affected directly by species diversity (e.g. species diversity does not affect the pressure gradients that set up winds and cause waves), the realized disturbance, or actual frequency, intensity or duration of biomass loss from a community, is often dependent on the diversity or species composition of that community (Pimm 1984; Tilman & Downing 1994; Tilman 1996; Mulder *et al.* 2001; Cardinale & Palmer 2002; Allison 2004).

Despite considerable research conducted on each of the unidirectional diversity–disturbance relationships, little is known about whether both relationships operate simultaneously. Here, we attempt to synthesize these two areas and explore how the reciprocal relationship between biodiversity and disturbance might produce feedbacks that alter expected patterns of diversity in nature. Indeed, as noted above, a previous review highlighted the high variability of the observed correlation between disturbance and diversity (Mackey & Currie 2001); feedbacks could be responsible for some of this variation. Specifically, we consider how diversity (which we use interchangeably with richness, without explicit consideration of specific species traits) might both change realized disturbance and be changed by disturbance severity. We define disturbance as any process that removes biomass from the community (Grime 1977), and thus disturbance severity is simply a measure of the fraction of biomass removed by the disturbance. We begin by reviewing experiments that have tested each direction of the diversity–disturbance relationship to illustrate the relative frequency of different causal relationships between these two factors. We then describe the results from several representative ecological systems in which disturbance has been separately shown to be both a cause and a consequence of local diversity and discuss the mechanisms responsible for these effects. Finally, we develop a conceptual model to explore how such reciprocal effects could either stabilize or destabilize diversity and evaluate the model over a range of demonstrated unidirectional relationships and disturbance severities. We focus our discussion on sessile, space-holding organisms as in the original formulation of the IDH.

EMPIRICAL SUPPORT FOR RECIPROCAL DIVERSITY–DISTURBANCE EFFECTS

To quantify the relative frequency of different relationships between diversity and disturbance, we conducted a comprehensive review of papers published from 1985 to 2006 using the ISI Science Citation Expanded Index database. We conducted separate searches for each of the unidirectional effects of diversity and disturbance using the following search terms: (i) species diversity or species richness, and disturbance or intermediate disturbance (i.e. Mackey & Currie 2001) and (ii) species diversity or species richness, and stability, resistance or resilience. We further limited both searches to experimental studies because correlations between diversity and disturbance cannot be unequivocally attributed to one unidirectional relationship or the other. A similar review of the effects of disturbance on diversity was conducted previously by Mackey & Currie (2001); however, this review included both observational and experimental studies while we were specifically interested in experimental effects. Furthermore, their study included only papers published through 1996 and thus we felt it was important to include the large number of studies published in the 10 years since their effort in order to facilitate comparison with studies of the effect of diversity on disturbance, most of which have been published since the mid-1990s (see Appendix S1 in Supplementary Material). We used the list in their study to capture experimental studies of the effects of disturbance on diversity published before 1985 (a total of nine studies). We also used their database to separately examine the frequency of possible disturbance–diversity relationships in observational studies, because these potentially reflect the outcome of both processes operating simultaneously.

Our searches yielded a combined total of 720 references. Based on the abstracts, we divided these references by response variable (diversity or disturbance response) and shape of the relationship [positive, negative, hump-shaped (IDH), u-shaped, not significant or other relationship]. When the abstracts were ambiguous, we examined the entire manuscript. As in Mackey & Currie (2001), experiments of disturbance effects on diversity needed to test at least three levels of disturbance in order to be included in our review. For studies that quantified both species diversity and species richness, we included only species richness as it is most comparable to our model. For the relationship between diversity and disturbance response, experiments had to include a specific disturbance event; experiments quantifying temporal stability or measures of variability were not included. We considered invasion by non-native species as a disturbance event, but we identify these studies separately in our results.

The results of our survey show that the most common effect of diversity is to reduce the impact of disturbance (Fig. 1a). Of the experimental tests of the effect of diversity on realized disturbance (64 references; Appendix S1), over 50% focused on the role of diversity in invasion resistance (Fig. 1a). As found by other reviews (e.g. Levine *et al.* 2004), experimental manipulations of diversity generally demonstrate that increasing diversity reduces invasion success. The distribution of effect frequencies differed little when invasion was compared to other disturbances such as drought or fire (Fig. 1a, $\chi^2 = 3.03$, $P = 0.22$), although the proportion of studies reporting 'no effect' did appear smaller for studies of invasion than for other disturbances.

Because diversity can either increase or decrease realized disturbance (Fig. 1a), formal meta-analysis to assess the 'average' effect size would seem unlikely to yield easily interpretable results (several strong positive and strong negative effects could yield zero net effect, leading to an erroneous conclusion of no effect of diversity on disturbance; cf. Stibor *et al.* 2004). Thus, in order to get a rough sense of the magnitude of positive and negative effects of diversity on disturbance, we calculated the proportional change in realized disturbance between low diversity and high diversity for each study in which the disturbance was something other than invasion (effect sizes for invasion have been previously calculated by Levine *et al.* 2004).

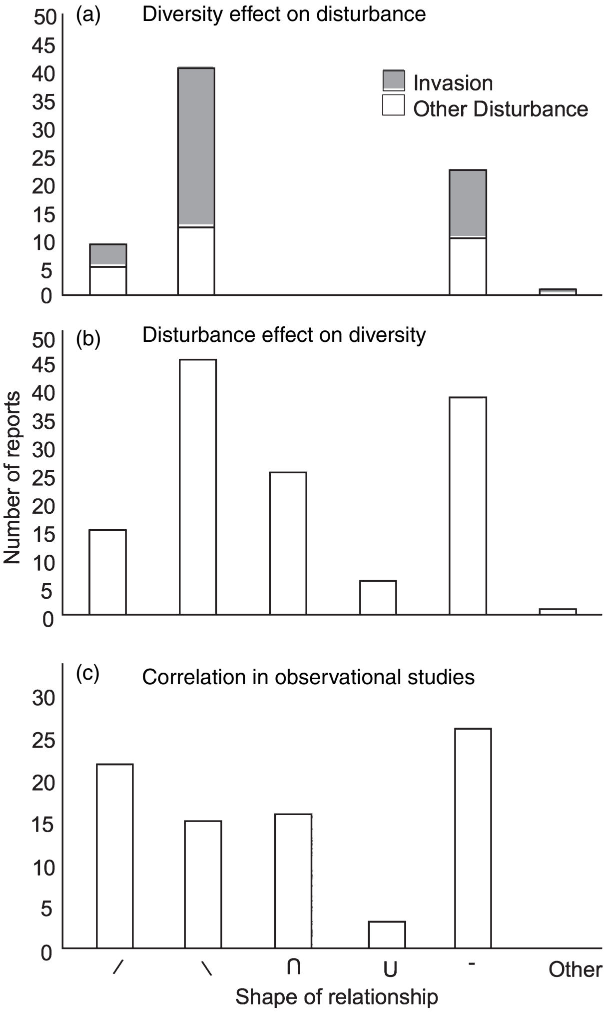

Figure 1 Frequency of different shapes of the relationships between diversity and disturbance as reported in published studies. (a) The effect of diversity on realized disturbance. Experiments examining diversity's effect on invasion success are shown in grey, others in white. A negative relationship indicates that diversity decreases realized disturbance or invasion (increases disturbance or invasion resistance). (b) Experimental effects of disturbance on species diversity. (c) Shape of correlation between disturbance (horizontal axis) and diversity (vertical axis) from observational studies in which neither diversity nor disturbance was manipulated. See text for details of literature search.

Among studies that identified a significant negative effect of diversity on realized disturbance (increased resistance or resilience), the median effect size was 0.32, with a range from 0.1 to 0.75. The median effect size in studies that identified a positive effect was smaller (0.24), although this estimate is based on only five studies.

There were 94 references (Appendix S2) that examined the effects of disturbance on species diversity or richness, yielding 130 relationships (Fig. 1b) illustrating that disturbance can have variable effects on diversity. Our findings generally agree with those of Mackey & Currie (2001) in that diversity does often affect disturbance (*c.* 70% of studies), but the shape is not consistently unimodal and a range of effects are possible. Experimental disturbance most commonly decreased or had no effect on species diversity (Fig. 1b), and the humped-shaped IDH pattern was only present in *c.* 18% of experiments. The frequency of different relationships is more evenly spread among possible outcomes in the observational studies included in Mackey & Currie (2001; Fig. 1c), with the most commonly reported significant relationship being positive, followed by unimodal and negative. Mackey & Currie (2001) discuss many possible reasons for the failure of both experiments and observations to consistently detect an IDH pattern, and we do not reiterate their excellent discussion here, as this is not the point of our paper. However, we note that because IDH patterns are associated with decreasing scale and increasing disturbance levels tested (Mackey & Currie 2001), it is likely that the absence of peaked relationships is partially explained by variation in experimental design. In addition, we argue below that reciprocal interactions between diversity and disturbance may also explain the low proportion of peaked relationships documented in the literature and the difference in the frequency of negative vs. positive relationships between experimental and observational studies (cf. Fig. 1b,c).

In addition to the evidence that diversity and disturbance can have a range of impacts on each other, we found numerous examples in which the unidirectional relationships between diversity and disturbance were independently documented in the same system and at the same spatial scale, raising the possibility that feedbacks could exist. We review a few of these examples here and provide a more complete list in Table 1. In terrestrial grasslands, for example, severe drought reduced species richness due to the loss of drought-susceptible species (Tilman & El Haddi 1992). Several of these plant species remained absent after 2 years of normal precipitation (Tilman & El Haddi 1992), suggesting that recruitment (or lack thereof) contributes to the effects of disturbance on diversity. Subsequent work showed that grassland species richness can influence realized disturbance, with more diverse plots exhibiting greater drought resistance (Tilman & Downing 1994). This negative effect of diversity on realized disturbance resulted because the plant species differed in their tolerance to drought, and because the species that survived the drought compensated through increased growth for those species that were lost (Tilman 1996).

Table 1 Ecological communities in which local-scale disturbance both affects and is affected by local diversity

System	Diversity affects disturbance response	Disturbance affects diversity
Coniferous trees	DeClerck *et al.* (2006*)	Loucks (1970*)
Intertidal macroalgae	Allison (2004)	Sousa (1979, 2001)
Kelp forest communities	Steneck *et al.* (2002), Byrnes *et al.* (2006)	Graham (2004), Goodsell & Connell (2005)
Seagrass invertebrates	Duffy *et al.* (2003)	Bostrom & Bonsdorff (2000)
Sessile marine invertebrates	Stachowicz *et al.* (2002)	Osman (1977), Lenz *et al.* (2004), Contardo Jara *et al.* (2006)
Stream invertebrates	Cardinale & Palmer (2002)	Lepori & Hjerdt (2006)
Terrestrial grassland	Tilman & Downing (1994)	Tilman & El Haddi (1992)

Communities with observational data only (marked with an *) are included to illustrate the potential range of systems in which feedbacks could be important. The list is not intended to be exhaustive and only representative studies are listed.

Marine macroalgal communities also provide evidence that diversity and disturbance can have reciprocal effects. Algae on intertidal boulders provide classic evidence in support of the IDH. In these communities, there is low algal diversity at high disturbance frequency due to the inability of many species to recruit and survive between disturbance events, low diversity at low disturbance frequency due to competitive exclusion, and high diversity at intermediate disturbance due to the coexistence of rapidly recruiting species and slower-growing competitive dominants (Sousa 1979). Additional studies also demonstrate the effects of physical or biological disturbance on algal species diversity (Lubchenco 1978; Carpenter 1981; Sousa 2001). On the other hand, algal species diversity reduces the resistance of some algal communities to disturbance (Allison 2004): high-diversity communities lost the most algal biomass as well as the highest proportion of algal cover to thermal stress, because these communities had the greatest amount of biomass to begin with and species did not show large variation in disturbance tolerance, although this may be in part due to the extreme nature of the disturbance. Despite this lowered resistance, more diverse communities exhibited greater resilience than did low-diversity plots, returning more rapidly to their pre-disturbance state. As in terrestrial grasslands, recruitment dynamics appear to be important; high-diversity plots may have recovered faster because they provided a local source of recruits to colonize the disturbed areas (Allison 2004). In this intertidal algal system, the unidirectional diversity–disturbance effects involve different types of disturbance (e.g. physical disturbance and heat stress); it is unclear how this difference might affect the degree and nature of diversity–disturbance feedbacks.

In sessile marine invertebrate communities, intermediate disturbance frequency and severity also maximize species diversity (Osman 1977). However, within these communities, the effect of disturbance on diversity can be contingent on the state of succession of the disturbed communities (Lenz *et al.* 2004), suggesting that variation in recruitment or community composition may impact disturbance-diversity relationships. Separate manipulations of diversity in this system also show that increasing diversity reduces fluctuations in community biomass, resulting in greater utilization of the limiting resource in this system (space), and thereby reducing community susceptibility to invasion by exotic species (Stachowicz *et al.* 2002). Thus, feedbacks between species diversity and disturbance might not only be common, but also complex and involve indirect interactions mediated through other ecosystem processes (Worm & Duffy 2003). Collectively, these examples and others (Table 1) suggest that greater consideration needs to be given to the possible stabilizing influence of a reciprocal relationship between diversity and disturbance.

A CONCEPTUAL APPROACH TO DIVERSITY–DISTURBANCE FEEDBACKS

The conceptual model

To our knowledge, no empirical study has simultaneously considered both directions of causality in the diversity–disturbance relationship. It is possible that if such studies were conducted, the unidirectional effects might differ dramatically in magnitude, such that one of the two dominates. Alternatively, the effects of different processes may be manifested at different spatial scales, as may be the case for reciprocal effects of diversity on productivity (Chase & Leibold 2002). However, if each effect were of similar magnitude and operated at the same scale, then feedbacks between the two might act in concert to affect patterns of diversity (Agrawal *et al.* 2007). As shown in the conceptual model illustrated in Fig. 2, such feedbacks could occur through a variety of processes documented in the literature that directly or indirectly link diversity and disturbance: (a) the effect of diversity on realized disturbance severity; (b) the effect of realized disturbance severity on diversity loss; (c) the effect of realized disturbance on subsequent recruitment and (d) the effect of realized disturbance on the intensity of competition. Processes (b–d) represent a decomposition of the effects that contribute to the influence of disturbance on diversity. Within this framework, the outcome of reciprocal diversity–disturbance effects can be assessed by sequentially examining how known relationships for each of these four processes affects diversity.

The simple relationships depicted in Fig. 2 combine to illustrate one possible diversity–disturbance feedback for which there is evidence in terrestrial plant communities. For example, in empirical work on terrestrial grassland species diversity (Tilman & El Haddi 1992; Tilman & Downing 1994; Naeem *et al.* 2000), these relationships take the following forms (see idealized plots within each component in the top panel of Fig. 2): (a) diversity decreases realized disturbance severity; (b) disturbance severity increases species loss; (c) diversity loss due to disturbance increases available resources, and thus increases the diversity of recruits and (d) low disturbance leads to intense competition and, thus, increased competitive exclusion. The result (shown in the bottom panel of Fig. 2) is a stabilizing feedback, in which the counteracting forces of diversity reducing the magnitude of realized disturbance, and low disturbance leading to competitive exclusion might cause communities to converge at intermediate levels of diversity.

The wide variety of relationships reported in the literature (Fig. 1) suggests that relationships (a–d) that link diversity and disturbance take a range of other forms in addition to those illustrated in Fig. 2, potentially leading to different outcomes. We discuss these possibilities below and in Fig. 3. We then present mathematical equations that represent the unidirectional relationships in our conceptual model to evaluate the consequences of different combinations of these relationships. We stress that these equations are not strict mechanistic representations of the ecological processes involved, but simply facilitate exploration of how all combinations of these relationships might affect diversity–disturbance feedbacks.

Variation in unidirectional relationships

The effects of diversity on realized disturbance

Our literature review revealed that there are a number of possible relationships describing the effect of diversity on realized disturbance (Fig. 1a). The impact of a given disturbance severity can be unaffected by diversity (Fig. 3ai), decrease with diversity (Fig. 3aii) or increase with diversity (Fig. 3aiii). The first two relationships are much more commonly found than the third (Fig. 1a). A lack of a

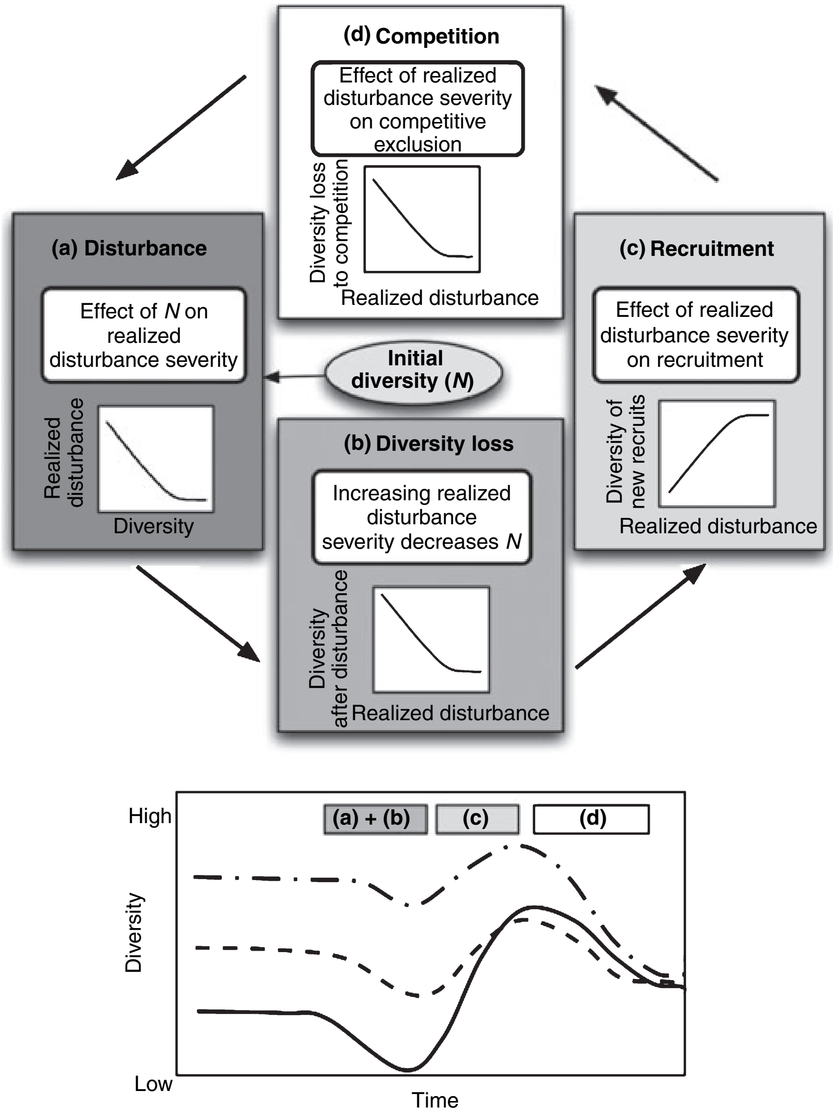

Figure 2 A conceptual model of diversity–disturbance feedbacks. Starting at initial diversity, four sequential unidirectional processes operating lead to feedbacks: (a) diversity affects realized disturbance, (b) disturbance increases diversity loss, (c) disturbance alters patterns of species colonization (recruitment) and (d) disturbance reduces the strength of competitive exclusion. In empirical work on terrestrial grassland species diversity (Tilman & El Haddi 1992; Tilman & Downing 1994; Naeem *et al.* 2000), the relationships take the form indicated in the plots within each box. Applying these relationships sequentially produces the trajectory of diversity over time depicted in the bottom panel, with the horizontal bars at the top of the figure indicating the portion of the time series during which each of the components (a–d) are in operation. Note that for these unidirectional relationships the result of feedbacks is convergence at intermediate levels of diversity.

diversity–disturbance relationship indicates a lack of reciprocity and thus a lack of the type of feedback on diversity depicted in Fig. 2; this occurred in about 1/3 of the studies reviewed. Additional shapes of this relationship are possible (e.g. complex nonlinear functions), but we limited ourselves to these three possibilities to simplify our initial approach and because few empirical studies have documented 'other' relationships (Fig. 1a).

The effects of realized disturbance on subsequent diversity

We partitioned the effects of realized disturbance on subsequent diversity into three separate processes operating sequentially: diversity loss (direct effect of biomass removal; Fig. 3b), recruitment (Fig. 3c) and competitive exclusion (Fig. 3d). We assumed that diversity loss increases with realized disturbance (Fig. 3b) and, thus, that there is a positive relationship between each of these and the amount of available resources.

We recognized two types of recruitment functions. Both fundamentally assume that recruitment is low at low disturbance severity because resident species prevent colonization by new species. As disturbance severity increases, more space (or other resource) is made available. Under one scenario this leads to a monotonic increase in recruitment of new species with increasing disturbance severity ('increasing' recruitment; Fig. 3cii; Stachowicz *et al.* 2002). When recruitment is low at high disturbance ('unimodal' recruitment, Fig. 3ci), recruitment peaks at some intermediate level of disturbance. In this case, as disturbance severity increases, fewer species can recruit successfully into a patch despite the available space, either due to a change in the physical characteristics of the patch (increased harshness leading to

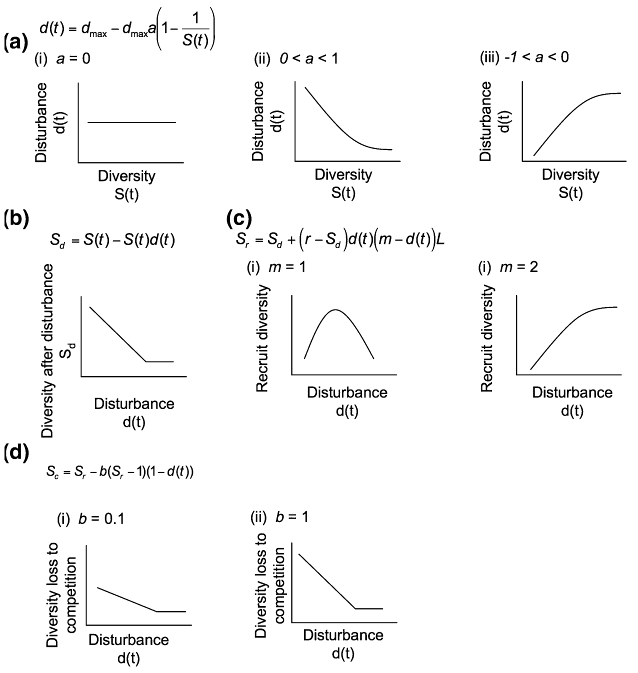

Figure 3 Variation in the shape of potential unidirectional relationships underlying diversity–disturbance feedbacks. Variation in the shape of the four relationships that form the basis of our conceptual model are illustrated in the figure. Simple, mathematical equations that quantitatively represent the unidirectional relationships were developed in order to facilitate the exploration of their combined consequences; these are presented with each conceptual figure and described in more detail in the text. (a) The effect of diversity on realized disturbance severity. (b) The effect of disturbance severity on diversity loss. (c) The effect of diversity loss on subsequent recruitment. (d) The effect of disturbance on the intensity of competition. Variable definitions: $d(t)$ = fraction of area cleared by disturbance at time t; $d_{\max}$ = severity of disturbance, unmodified by diversity; a = proportion of disturbance that is affected by diversity; $S(t)$ = diversity at time t; S_d = diversity after disturbance; S_r = diversity after recruitment; r = regional pool size ($r = 40$ in all analyses); m = the strength of recruitment limitation at high disturbance; L = the maximum proportion of the regional species pool that is present when the community is saturated; b = strength of competition.

poor establishment, e.g. Dudgeon & Petraitis 2001) or effects on propagule supply as densities or reproductive output of species in the region decline across the board in response to disturbance (dispersal limitation). Alternatively, a unimodal disturbance–recruitment diversity relationship might result under a scenario of inhibition or facilitation succession, or when there is some sort of trade-off between competitive ability and colonization success, whereas recruit diversity might increase monotonically with disturbance under a 'tolerance' or 'initial floristic composition' model of post-disturbance succession.

Finally, we considered how post-disturbance competition alters diversity. We assumed that increased disturbance would decrease the strength of competition by freeing up space and resources (Sousa 2001). We examined the model under conditions of both strong (Fig. 3di) and weak (Fig. 3dii) competition. Strength of competition in this context refers to the degree to which competitive exclusion causes diversity loss.

Evaluating the conceptual model

We evaluated our model under a range of conditions by running simulations using mathematical expressions of the conceptual relationships from Fig. 3 to explore how different combinations of diversity, disturbance, recruitment and competition affect the reciprocal relationship between diversity and disturbance. The equations are defined below and listed in Fig. 3 for convenience. We assumed that disturbance occurs first, leading to diversity loss, followed by recruitment that increases diversity, and then competitive exclusion that will again lower diversity. Realized disturbance is defined (Fig. 3a) as the fraction of area of a patch that is cleared of all individuals at a given point in time, $d(t)$, where

$$d(t) = d_{\max} - d_{\max}a\left(1 - \frac{1}{S(t)}\right) \quad (1)$$

It is dependent on the species diversity of a patch, $S(t)$, the absolute severity (i.e. spatial extent) of the disturbance unmodified by local diversity, $d_{\max}$, and a coefficient describing the proportion of the absolute disturbance ameliorated by diversity, a. We explore three different scenarios: if $a = 0$, diversity has no net effect on the disturbance (Fig. 3ai); if $0 < a < 1$, then diversity decreases realized disturbance (Fig. 3aii) and if $-1 < a < 0$, then diversity increases realized disturbance (Fig. 3aiii).

After determining the level of realized disturbance, diversity within a patch is affected sequentially by three processes. First, diversity is lost to realized disturbance (eqn 2; Fig. 3b), with $S(t)$ representing species diversity at time t before disturbance and S_d as diversity after disturbance so that

$$S_d = S(t) - S(t)d(t) \quad (2)$$

Following the loss of diversity from disturbance, species are gained owing to recruitment (Fig. 3c). New species are able to colonize cleared patches so that S_r, diversity after recruitment is a function of r, the regional pool size, S_d, diversity after disturbance, and then modified by the amount of realized disturbance, $d(t)$.

$$S_r = S_d + (r - S_d)d(t)(m - d(t))L \quad (3)$$

The second part of the equation defines what proportion of the propagule pool can colonize the patch as modified by disturbance. As *d(t)* increases, more space is opened up, so more new species may colonize a patch. As outlined above, as disturbance increases recruitment diversity may be limited by several factors, such as dispersal limitation or harsh conditions. The strength of these limiting factors can vary, and are represented in our model by m. If $m = 1$, then no species can recruit at the highest level of realized disturbance ($d(t) = 1$). If $m = 2$, then there is no limitation at full strength disturbance and recruitment increases linearly with disturbance. We refer to these as 'unimodal' and 'increasing' recruitment, respectively, and we consider both cases in our model (Fig. 3ci,cii). Because S_r in this equation peaks at 25% of the regional richness (rather than 100%, see Fig. 3ci) when $m = 1$, we introduced a term, L, which can scale recruitment up to the full number of remaining species in the species pool ($r - S_d$). We used a value of $L = (2/m)^2/2$ which assumes that community saturation occurs at a diversity level lower than the regional pool size. Different values of L do not qualitatively change our results (data not shown).

Both newly recruited species and previously established ones can be lost to competitive exclusion (eqn 4; Fig. 3d). We assume that most of the competition comes from the adults that remained post-disturbance, and thus allow competition to decrease with increasing disturbance due to increased resource availability (Sousa 2001). Diversity following competition (S_c) therefore can be described by eqn 4, where b is a competition coefficient.

$$S_c = S_r - b(S_r - 1)(1 - d(t)) \qquad (4)$$

Here, we examine both weak (Fig. 3di) and strong (Fig. 3dii) competition, reflecting either variation in the degree of competitive exclusion at a given spatial scale or across spatial scales (with large values likely more prevalent at small patch sizes, and small values at the larger site scale; Russell *et al.* 2006).

While many possible scenarios could be evaluated using our conceptual model, we focused on two main areas in which we felt feedbacks might actually operate in nature. First, we generated predictions of diversity dynamics for different initial diversity levels (i.e. low, intermediate or high) through three iterations of disturbance at low ($d_{\max} = 0.2$), intermediate ($d_{\max} = 0.5$) or high ($d_{\max} = 0.8$) disturbance severity. Second, we explored how varying both initial diversity and the fraction of patch area cleared by disturbance (i.e. severity) affects the relationship between disturbance and diversity in the presence and absence of disturbance-diversity feedbacks. We set the proportion of the absolute disturbance that was affected by diversity (a in eqn 1) at 0.35, which approximates the median size of positive diversity effects on disturbance severity in our literature survey.

INSIGHTS FROM THE CONCEPTUAL MODEL

Figure 4 illustrates expected changes in diversity under strong disturbance ($d_{\max} = 0.8$) for a range of initial diversity levels. Comparing panel (4i) with the bottom panel of Fig. 2 reveals that the predictions of the model match our conceptual expectations based on sequentially applying unidirectional relationships derived from empirical work in grasslands. Several generalizations emerge from our model results; these results did not differ qualitatively based on the severity of disturbance (see Figs S1 and S2 for low and intermediate disturbance, respectively). First, initial diversity can influence the trajectory of diversity over the short-term (i.e. 2–3 rounds of disturbance), particularly when diversity reduces realized disturbance (Fig. 4c,f,i,l). In contrast, increasing realized disturbance with diversity quickly negates variation due to initial diversity when recruitment is high at high disturbance (i.e. increasing; Fig. 4g,j). Finally, feedbacks in which diversity increases realized disturbance can result in patch-level extinctions when recruitment is low at high levels of disturbance (i.e. unimodal; Fig. 4a,d).

In addition to diversity at a single point in time, temporal variation in diversity is an important feature of communities that can be altered by the reciprocal relationship between diversity and disturbance (Fig. 4). For example, the presence and sign of diversity effects on realized disturbance alter the ultimate level of diversity attained over time under a unimodal recruitment scenario. In this case, a positive effect of diversity on disturbance (i.e. $a < 0$) causes all plots to quickly converge to low diversity or go extinct (Fig. 4a,d), while a reduction of realized disturbance with diversity ($a > 0$) leads to higher average levels of diversity (Fig. 4c,f) than when there is no feedback (Fig. 4b,e). Feedbacks also appear to affect the degree of variability in diversity, as the magnitude of change in diversity over time is sometimes smaller over a single round of disturbance when diversity decreases realized disturbance than when it increases disturbance, especially with unimodal recruitment (Fig. 4a,c,d,f).

To assess how feedbacks alter the effect of changing disturbance severity on diversity (e.g. How do feedbacks affect support for the IDH?), we explored the impact of a single round of disturbance of varying severity on diversity for three representative values of a and different levels of initial diversity (Fig. 5). We focus on one disturbance event because most experimental tests of the effect of disturbance on diversity examine a single pulsed disturbance. Some, but not all, combinations of unidirectional relationships can yield an IDH pattern. Specifically, the hump-shaped pattern is most common when diversity increases or has no effect on realized disturbance severity, and recruitment is low at high disturbance (i.e. unimodal; Fig. 5a,b,d,e). In contrast,

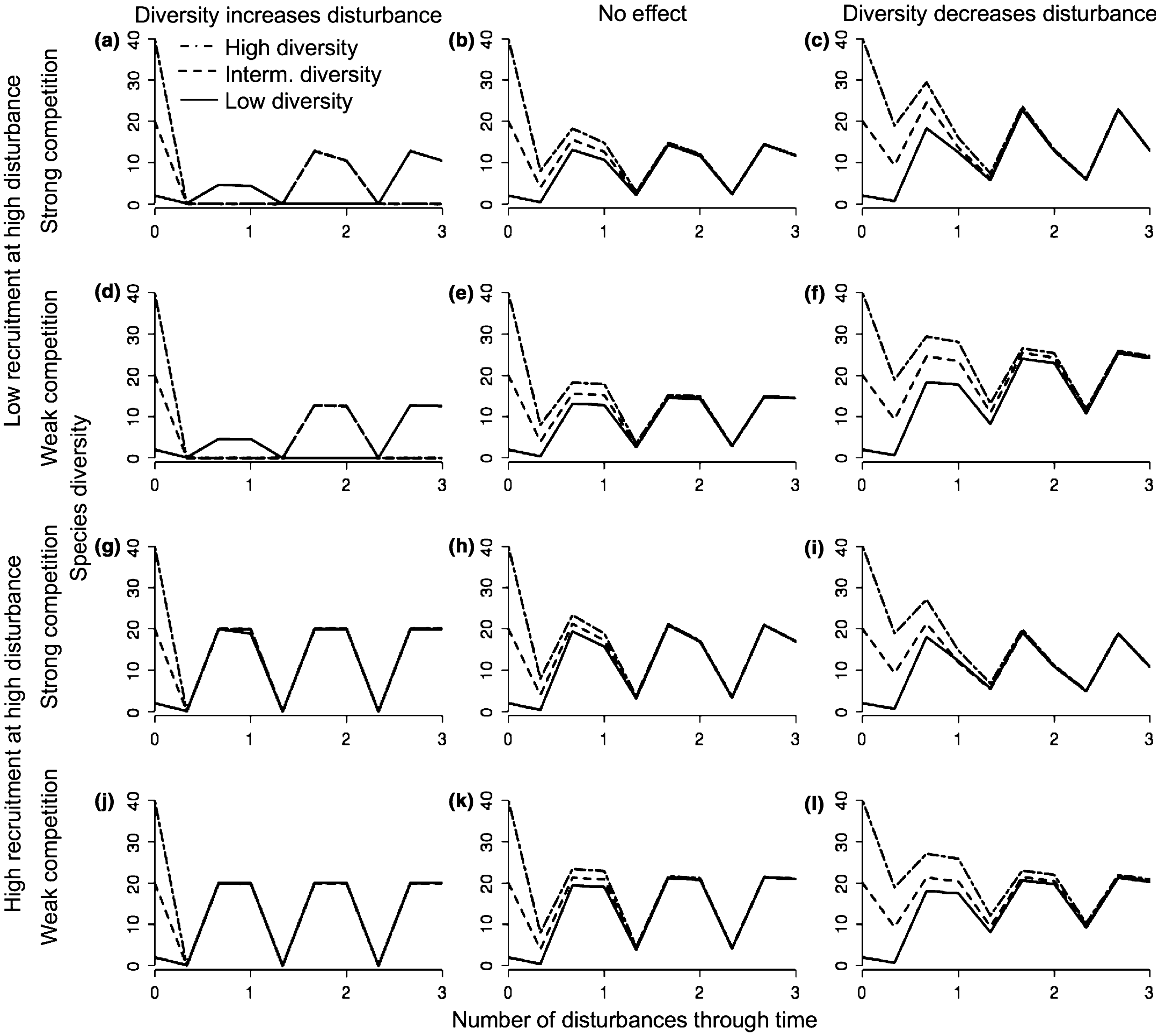

Figure 4 Diversity change over time as predicted by the conceptual model. Change in diversity across three high disturbance events ($d_{\max} = 0.8$) with diversity increasing disturbance ($a = -0.35$), having no effect on disturbance ($a = 0$), or diversity ameliorating disturbance ($a = 0.35$). Different lines on each panel represent three levels of initial diversity: high (40 species, dot-dashed lines), intermediate (20 species, dashed lines) and low (two species, solid lines) with a regional pool size (r) of 40. The first disturbance occurs at time = 0; this disturbance causes a decrease in diversity, followed by an increase owing to recruitment and then a decrease owing to competitive exclusion. The top two rows (a–f) show curves when recruitment is limited at high disturbance ($m = 1$; 'unimodal' recruitment). The bottom two rows (g–l) show curves for when recruitment is highest at high disturbance ($m = 2$; 'increasing' recruitment). Competition is strong ($b = 1$) in panels (a–c) and (g–i). Competition is weak ($b = 0.1$) in panels (d–f) and (j–l). Patterns under low or intermediate disturbance are illustrated in Figs S1 and S2.

when diversity decreases realized disturbance, diversity tends to increase across the disturbance gradient (Fig. 5c,f,i,l), particularly at low and intermediate initial diversities. This relationship even occurs with unimodal recruitment (Fig. 5c), suggesting it is not merely the result of a particular disturbance–recruitment relationship.

To better illustrate the conditions under which feedbacks enhance vs. suppress diversity, we re-plotted curves from Fig. 5, overlaying results of positive ($a = -0.35$), negative ($a = 0.35$) and no effect ($a = 0$) of diversity on realized disturbance (Fig. 6). The effect of reciprocal relationships on diversity is most evident at intermediate and higher

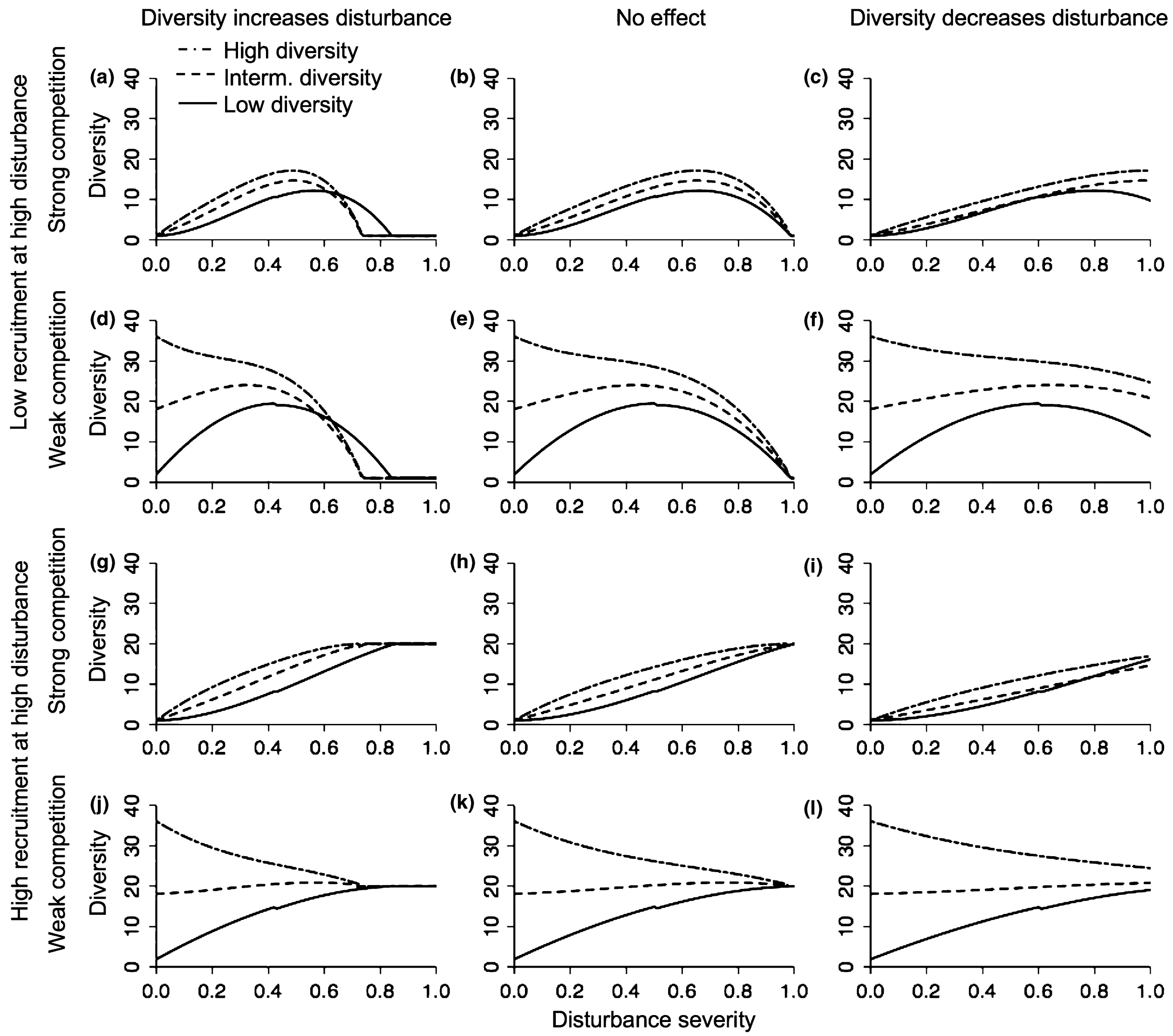

Figure 5 Diversity–disturbance feedbacks affect the likelihood of observing patterns of diversity and disturbance consistent with the intermediate disturbance hypothesis. Panels show the effect of varying the effect of diversity on realized disturbance on the predicted relationship between disturbance severity and diversity when diversity increases disturbance ($a = -0.35$), has no effect on disturbance ($a = 0$), or diversity ameliorates disturbance ($a = 0.35$). Different lines on each panel represent differing initial diversity: high (40 species, dot-dashed lines), intermediate (20 species, dashed lines) and low (two species, solid lines). The top two rows (a–f) show curves when recruitment is limited at high disturbance ($m = 1$; 'unimodal' recruitment). The bottom two rows (g–l) show curves for when recruitment is highest at high disturbance ($m = 2$; 'increasing' recruitment). Competition is strong ($b = 1$) in panels (a–c) and (g–i). Competition is weak ($b = 0.1$) in panels (d–f) and (j–l). Regional species pool size (r) is 40.

disturbance severity (Figs 5 and 6), because when disturbance is weak, its direct effect on diversity is also weak, and thus initial diversity most strongly determines final diversity. In addition, the shape of the disturbance–recruitment relationship is a key aspect of understanding when feedbacks will be important in maintaining diversity. When recruitment is unimodal (Fig. 6a,b) and disturbance severity is moderate to high, a reduction in realized disturbance with increasing diversity results in higher diversity than when there is no feedback. Correspondingly, when diversity increases realized disturbance, diversity following disturbance is lower than predicted when there is no feedback. Interestingly, the opposite pattern occurs when recruitment increases with disturbance and there is strong competition (i.e. highest diversity is attained when diversity enhances disturbance; Fig. 6c). This difference occurs because

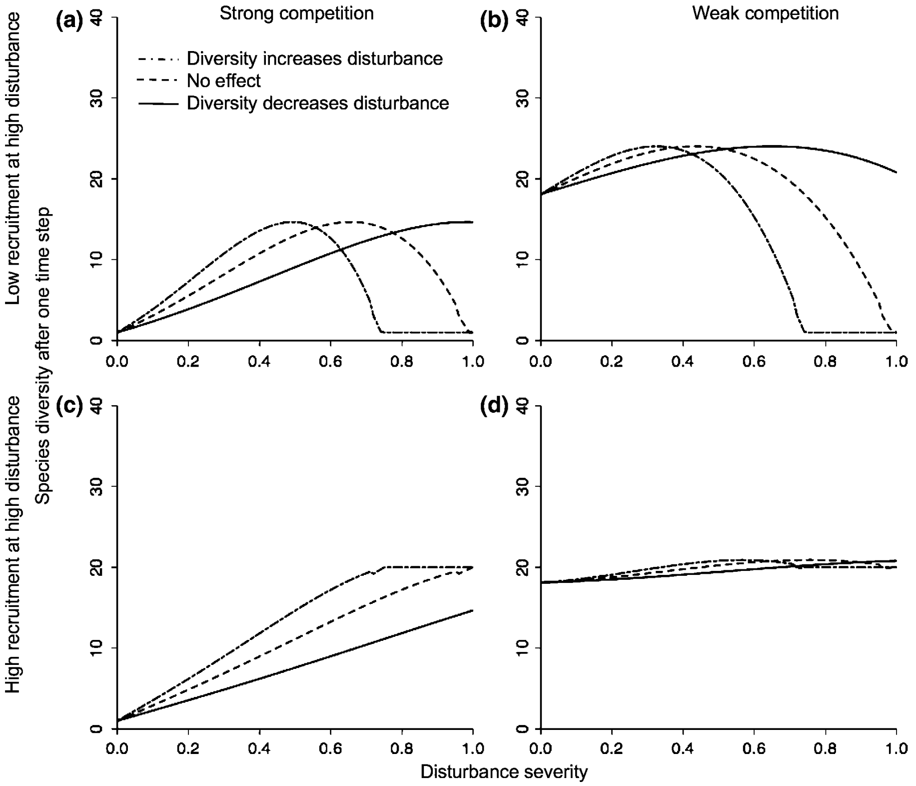

Figure 6 Relationship between diversity severity and disturbance for cases of positive, negative and no effect of diversity on realized disturbance. Panels show patterns of how diversity after one round of disturbance, recruitment and competition as a function of disturbance severity. Initial diversity was 20 species. Solid lines indicate that diversity decreases realized disturbance ($a = 0.35$), dashed lines show no effect of diversity on disturbance ($a = 0$) and dot-dashed lines are when diversity increases realized disturbance ($a = -0.35$). (a and b) Recruitment is low at high disturbance ($m = 1$; 'unimodal' recruitment). (c and d) Recruitment is high at high disturbance ($m = 2$; 'increasing' recruitment). In panels (a and c), competition is strong ($b = 1$). In panels (b and d), competition is weak ($b = 0.1$). Regional species pool size (r) is 40.

communities where recruitment is high at high disturbance (i.e. increasing recruitment; Fig. 6c,d) receive the highest recruitment of new species under high disturbance, but this is not the case when recruitment is low at high disturbance (i.e. unimodal recruitment; Fig. 6a,b). When competition is strong (Fig. 6c) it leads to greater loss in areas that lost fewer species to disturbance (i.e. where diversity decreases or has no effect on realized disturbance), causing overall diversity to decrease as one moves from positive to negative effects of diversity on realized disturbance. Differences due to feedbacks disappear with increasing recruitment and weak competition (Fig. 6d), because each unidirectional effect is weak, and because the initial diversity level depicted in Fig. 6 (20 species, or half the regional pool) is also close to the diversity level that this particular competition-recruitment scenario will converge. Indeed, for patches with weak competition in general, the relationship between diversity and disturbance is highly dependent on initial diversity (Fig. 5d–f,j–l).

To get a more complete picture how the strength of diversity effects on realized disturbance influences the predicted correlations between disturbance and diversity, we examined final diversity (given intermediate initial diversity) after one round of disturbance, recruitment and competition across the range of possible values of a ($-1.0 < a < 1.0$; Fig. 7). These results confirm the patterns in Fig. 5, illustrating that the relationship between disturbance and diversity (positive, hump shaped or negative) will be highly contingent on the strength and direction of the diversity–disturbance relationship if recruitment is unimodal. In general, a positive relationship between disturbance and diversity is most common when diversity reduces realized disturbance (dark grey shading; Fig. 7a,b), although it occurs regardless of the presence of a reciprocal relationship when there is increasing recruitment and competition is strong (Fig. 7c). The same result does not occur under weak competition (Fig. 7d) for this particular level of species diversity (i.e. 20 species), although for other levels of initial

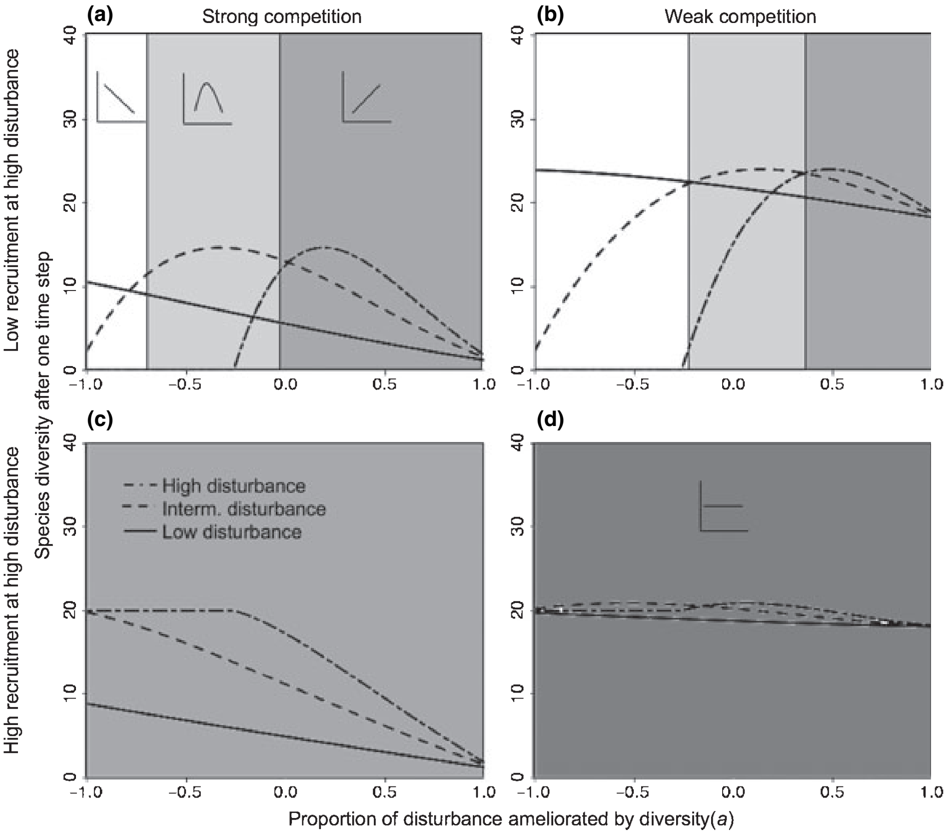

Figure 7 The strength and direction of the effect of diversity on realized disturbance alters diversity after one round of disturbance, recruitment and competition. Initial diversity was 20 species. Solid lines denote low disturbance ($d_{\max} = 0.2$), dashed lines are intermediate disturbance ($d_{\max} = 0.5$) and dot-dashed lines are high disturbance ($ds_{\max} = 0.8$). The resulting relationship between disturbance (x axis) and diversity (y axis) that corresponds with Fig. 1b is indicated by shading and the inset figures: diversity that decreases with disturbance (no shading); a hump-shaped relationship between diversity and disturbance as predicted by the intermediate disturbance hypothesis (light grey shading) diversity that increases with disturbance (intermediate grey shading) or no relationship (dark grey shading). (a and b) Recruitment is low at high disturbance ($m = 1$; 'unimodal' recruitment). (c and d) Recruitment is high at high disturbance ($m = 2$; 'increasing' recruitment). In panels (a and c), competition is strong ($b = 1$). In panels (b and d), competition is weak ($b = 0.1$). Regional species pool size (r) is 40.

diversity, Fig. 7d is qualitatively similar to Fig. 7c (e.g. see Fig. 5j,k,l). A hump-shaped relationship as predicted by the IDH occurs when diversity increases or has no effect on realized disturbance (light grey shading; Fig. 7a,b). Thus, an IDH pattern appears more likely in the absence of a reciprocal effect of diversity on realized disturbance. Decreasing diversity with increasing disturbance is only predicted when diversity increases realized disturbance and there is unimodal recruitment, and it occurs over a broader range of negative values of *a* when competition is weak (unshaded areas, Fig. 7a,b).

DISCUSSION

Evidence for reciprocal diversity–disturbance effects from published experiments (Fig. 1), combined with our simple conceptual model (Fig. 2), suggests that feedbacks between diversity and disturbance could influence patterns of diversity in nature. At present, we do not know enough about the specific relationships between diversity, disturbance, competition and recruitment in any particular system to evaluate the impact of feedbacks empirically. However, in systems where one of the unidirectional relationships between diversity and disturbance is clearly documented, our model may provide some insight into the reciprocal relationship. For instance, plant species diversity decreases realized disturbance in terrestrial grasslands (Tilman & Downing 1994); our model predicts that increasing disturbance likely leads to increasing diversity in these systems, regardless of the specific recruitment or competition dynamics (Fig. 7). On the other hand, intertidal macroalgal systems provide some of the best-known examples of the IDH (Sousa 1979, 2001). Based on this relationship, our model results suggest that these systems are characterized by unimodal recruitment (Fig. 7a,b) and (i) diversity increasing disturbance when competition is strong (Fig. 7a) or (ii) weak effects of both competition and diversity on disturbance (Fig. 7b). The one known test of the effects of intertidal algal diversity on realized disturbance provides some support for the second scenario, with diversity decreasing the resistance but increasing the resilience of algal plots to disturbance (Allison 2004), perhaps leading to an overall weak effect of diversity on disturbance.

From a practical perspective, the fact that diversity can vary greatly over the disturbance and recovery process (Fig. 4), often depending on initial conditions, indicates that sampling intervals and experiment duration are crucial for interpreting the relationship between diversity and disturbance (Shea *et al.* 2004). The perceived effects of disturbance on diversity may thus vary as a function of time since the last disturbance or successional state (e.g. Lenz *et al.* 2004). In addition, when feedbacks exist, disturbances of equivalent initial strength can differentially impact communities of different composition, as realized disturbance can be modified in various ways by different levels of initial species diversity (Fig. 5). Finally, because specific conditions of disturbance, diversity, recruitment and competition are needed in our model to generate the phenomenon of maximum diversity at intermediate disturbance severity (i.e. IDH), diversity–disturbance feedbacks could offer an explanation for some of the variation in field patterns of diversity along disturbance gradients that was previously considered 'noise' (Mackey & Currie 2001).

We find it interesting that both our review and others reveal that the most commonly reported experimental effect of disturbance on diversity is negative rather than hump-shaped (Fig. 1b). However, it is difficult to link our model outputs with the outcome of the experimental studies in our literature review that manipulate disturbance; these studies often control realized disturbance directly, by design minimizing the opportunity for initial diversity to affect the outcome except through speed of recovery (resilience). Even in the experiments that manipulate potential rather than realized disturbance by, for example, varying grazer density, the impacts of diversity on disturbance resistance are limited because most experiments begin with plots of similar diversity to avoid confounding the interpretation of results. In fact, looking at the distribution of results of observational studies only (Fig. 1c), which should include both parts of the reciprocal relationship, suggests that a negative disturbance-diversity relationship is not as common as no relationship or a positive relationship (see also Mackey & Currie 2001). Rather, the positive relationship is the most commonly reported significant relationship. Our model suggests that such a relationship could result from either high recruitment at high disturbance with strong competition (a tolerance model of succession) or when diversity reduces realized disturbance (Fig. 5a,c). Other processes may produce such a relationship as well, and the relative importance of these scenarios is unknown. Of course, some disturbances will be strong enough to overcome biotic resistance (e.g. hurricanes, bulldozers or human experimenters) and thus diversity is unlikely to increase indefinitely. More empirical data on whether these feedbacks operate is clearly needed.

Our model suggests a number of novel reasons why the hump-shaped diversity pattern predicted by the IDH may not be the most common result in disturbance experiments (Figs 5 and 7). When competition is strong, increasing disturbance with increasing diversity is needed to meet the predictions of the IDH (Fig. 7a). The low number of experiments demonstrating negative effects of diversity on disturbance resistance (Fig. 1a) suggests that this effect may not be common in nature. In addition, when diversity decreases, or has no effect on, realized disturbance (*c.* 90% of experimental tests), weak, not strong, competition leads to a hump-shaped relationship. Given the importance of competitive exclusion to the formulation of the IDH, there may be a bias towards testing for this pattern in communities with strong competition.

Perhaps more than providing definitive answers, we hope our review and model will stimulate additional thought and experimentation on diversity–disturbance feedbacks. Here, we note several areas that appear to us to warrant future investigation. First, we assumed that disturbance, diversity loss, recruitment and competition occur as discrete events in fixed order, such as in a seasonal environment with short-lived species (e.g. sessile marine invertebrates). However, in some systems disturbance and competitive exclusion may occur less frequently than recruitment, or recruitment could be a relatively rare event. Thus, it will be interesting to examine the dynamics that result when the order and frequency of the processes in our model vary, though we felt this was beyond the scope of exploration in this paper. Second, we focused solely on disturbance severity in this discussion; future research should consider scenarios where disturbance varies in frequency as well as severity, potentially weakening the direct feedback between diversity and disturbance despite the presence of both independent unidirectional relationships. Within our conceptual model this could be accomplished in principle by re-applying the disturbance before recruitment or competition take place. In addition, our model also centred around a 'patch' in which disturbance, the strength of competitive exclusion and recruitment limitation were homogeneous. Variation in spatial and temporal processes can have dramatic consequences for coexistence and species dynamics within ecological communities (Chesson 2000a,b). Feedbacks could have very different emergent consequences at larger scales if all three parameters are allowed to vary within space and time. Furthermore, here we only consider diversity within a trophic level or guild, but we note reciprocal relationships might operate across trophic levels too. For example, it is well known that consumers affect prey diversity, but prey diversity might also affect consumer persistence since at low diversity of prey species, any loss of species might cause consumers to lose their only remaining prey, resulting in a cascade of extinction (Ebenman *et al.* 2004). Similarly, changes in predator diversity can have cascading effects on prey diversity (Dyer & Letourneau 2003). How might changes in predator diversity due to disturbance affect prey, and do predators and prey differ in how their diversity may alter realized disturbance? Finally, analogous reciprocal relationships could occur between genetic diversity in clonal organisms and disturbance, as each of the unidirectional relationships have been demonstrated, though not in the same system (Weider 1992; Buckling *et al.* 2000; Hughes & Stachowicz 2004; Reusch *et al.* 2005). However, the inherent differences in recruitment of genotypes (which arise *de novo* via sexual reproduction) and species will require some modifications to our conceptual approach.

CONCLUSION

We suspect that reciprocal processes operating on the same scale will eventually be recognized to be as common for other community-level processes as they currently for population processes (Agrawal *et al.* 2007). For instance, an easy to envision example is the relationship between diversity and community invasibility. The invasion of a community directly increases species richness by one, but it can also lead to indirect decreases in local diversity due to competitive effects (Bruno *et al.* 2005) or further increases due to facilitation (Bruno *et al.* 2005; Rodriguez 2006). Because diversity, *per se*, usually leads to reduced invasion susceptibility (Fig. 1a, see also Levine *et al.* 2004), feedbacks in either direction can occur; successful invasion may simply increase diversity and enhance biotic resistance incrementally, or it could decrease diversity and enhance invasion risk. Furthermore, disturbance or productivity also usually affect both invasion and diversity independently (Elton 1958; Lozon & MacIsaac 1997; Naeem *et al.* 2000; Mittelbach *et al.* 2001), raising the possibility of more complex feedbacks in which, for example, adding resources reduces diversity which then facilitates invasion, which might further reduce local diversity [see Discussion in Maron & Marler (in press) for a possible example]. Similarly, complex feedbacks between diversity, productivity and disturbance have been proposed (Worm & Duffy 2003).

Understanding community-level feedbacks such as those involving diversity and disturbance has implications for understanding the response of ecological systems to human perturbation. Given that humans are at the same time directly decreasing diversity and increasing disturbance, the existence of feedbacks suggests that these stressors could act synergistically (Fig. 6): the result could be an acceleration of species loss beyond the expectations of direct human modification of habitats. Ecologists have long recognized that environmental factors can affect the maintenance of biodiversity. The more recent recognition that particular species and even species diversity can influence these same factors suggests that broad consideration of reciprocity and feedbacks might be needed to adequately predict how biodiversity and ecosystem services will be altered by human activities. Diversity–disturbance is but one example of the way in which reciprocal ecological relationships and feedbacks can challenge our simple predictions.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Experiments examining the effect of diversity on realized disturbance.

Appendix S2 Experiments examining the effects of disturbance on diversity.

Figure S1 Diversity change over time at low disturbance as predicted by the conceptual model.

Figure S2 Diversity change over time at intermediate disturbance as predicted by the conceptual model.

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