REVIEW

Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes

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Abstract

Coexistence mechanisms that require environmental variation to operate contribute importantly to the maintenance of biodiversity. One famous hypothesis of diversity maintenance under disturbance is the intermediate disturbance hypothesis (IDH). The IDH proposes patterns of peaked diversity under intermediate disturbance regimes, based on a tension between competitively superior species and species which can rapidly colonize following disturbance. We review the literature, and describe recent research that suggests that more than one underlying mechanism can generate this unimodal diversity pattern in disturbed environments. Several exciting emerging research areas are identified, including interactions between disturbance types, operation of the IDH in multi-trophic systems, and changes in disturbance regimes. However, empirical work is still focussed on describing the IDH pattern, with little emphasis on identifying its mechanistic basis. We discuss how to extend methods for identifying different coexistence mechanisms, developed in the theoretical literature, to experimental research. In an attempt to operationalize these various ideas we outline a hypothetical IDH research programme. A solid understanding of the life history attributes of the component species and their responses to disturbance will facilitate identification of the coexistence mechanism(s) underlying the IDH pattern, and provide a framework by which empirical and theoretical results can be more fully integrated.

Keywords

Coexistence, disturbance, intermediate, intermediate disturbance hypothesis, relative nonlinearity, storage effect.

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INTRODUCTION

Species coexistence

Elucidating the many ways in which species can coexist is one of the most exciting central problems in community ecology. More than half a century of work on species coexistence has generated consensus on the importance of classic mechanisms, such as resource partitioning, that operate independently of environmental fluctuations (Tilman 1982; Chesson 2000b). However, there are strong but divergent opinions on which additional factors generate and maintain natural biodiversity in fluctuating environments, and on how to organize our view of such mechanisms (Huston 1979, 1994; Chesson & Huntly 1997; Chesson 2000b; Hubbell 2001). Historically, ecologists began by averaging over environmental variability, treating it as background noise, and focusing solely on fluctuation-independent mechanisms of coexistence. However, it is now well established that environmental variability is an integral part of the dynamics of natural systems, including mechanisms of species diversity.

In this review we focus on one particular aspect of coexistence-promoting environmental variation. The intermediate disturbance hypothesis (IDH) encapsulates the idea that coexistence and/or biodiversity peak under intermediate disturbance regimes (Fig. 1). Too much disturbance, and longer-lived species cannot persist in the system; too little disturbance, and competitive superiors drive pioneer species to extinction. Only between these extremes, at intermediate levels of disturbance, can both types coexist.
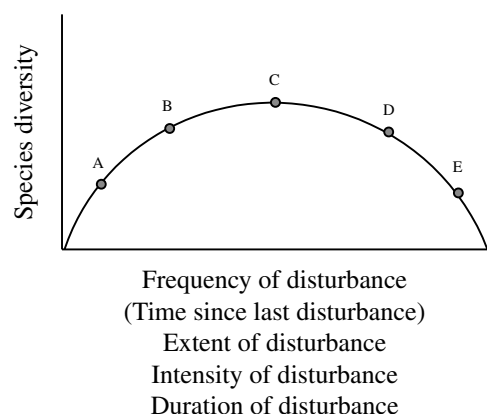
Figure 1 Hypothesized relationship between species diversity and a series of disturbance attributes as suggested by the IDH. The unimodal curve suggests a peak in number of species at intermediate disturbances. See text for further details.

History of the IDH

While older work linked disturbance and species coexistence (Hutchinson 1951, 1953, where he attributes a similar idea to Elton), the first clear references to the effect of intermediate disturbances on biodiversity arose in the 1970s [Grime 1973a,b; Connell 1978, 1979; see also the Fox & Connell (1979) dialogue and Wilkinson (1999)]. Since that time a myriad of papers have addressed the ways in which disturbance regimes affect various aspects of species diversity, such as the short-term impact of disturbance on community diversity, or the long-term stable coexistence of species (see Tables 1 and 2). Here we focus solely on the role of disturbance as a promoter of long-term stable species coexistence.

What is a disturbance?

Commonly cited types of disturbance include: hurricanes, fires, hailstorms, tree falls, landslides, waves, mowing, digging, grazing or predation, trampling, fragmentation, drought and floods (Sousa 1984, Table 1a). What do all of these occurrences have in common? There have been many, more or less related, definitions of disturbance (Begon *et al.* 1990; van der Maarel 1993; Roxburgh *et al.* 2004). We define a disturbance as an event which alters the niche opportunities (*sensu* Shea & Chesson 2002) available to the species in a system. This will often be an event which destroys or removes biomass, freeing up resources for other organisms to use. However, it could also be a direct shift in available nutrients, or more generally, any other event that impacts on the niche relationships of the organisms.

Recent insights and new directions

Recent work has suggested a number of new angles from which to profitably address the IDH. A fundamental recent insight is that the IDH pattern of maximum diversity under intermediate disturbance can arise from different underlying mechanisms (Sheil & Burslem 2003; Roxburgh *et al.* 2004). These mechanisms can be described in biological or mathematical terms (see below). For this reason, we need to move to a more rigorous understanding of the underlying mechanisms occurring in disturbed systems in order to properly describe the scope (when would we even expect the IDH to operate?) and effects of the phenomenon, and in order to improve our ability to predict outcomes.

Achieving these goals demands a combination of theoretical (including modelling), experimental and observational studies. Whilst combining a range of approaches is generally seen to be advantageous for many scientific endeavours, for disentangling the mechanisms underlying the IDH we argue that it is an absolute necessity. Research programmes designed without an appreciation of the possible range of underlying mechanisms may fail to ask the correct question, or may just describe the phenomenon without generating deeper insight. Not only can new work be planned to include these latest insights, but much previous work can be re-evaluated in the light of an awareness of such mechanisms (although often this will have to be done by the original researchers as vital information is not always presented in publications, as found in our review below).

In the remainder of this paper we review and describe the implications of these possibilities. As well as describing theoretical and empirical issues relating to the underlying mechanisms, we discuss the ways in which disturbances and their intermediacy can be defined and operationalized, and the circumstances under which IDH patterns might be expected in real systems. In the context of these discussions we then survey the current literature, briefly outlining some exciting new areas of research highlighted by the review. We conclude with the outline of a research design for one system, using this as a forum for integrating these theoretical and empirical developments. In particular, we extend methods developed for differentiating between different coexistence mechanisms underlying the IDH in theoretical studies (e.g. Roxburgh *et al.* 2004) to application in experimental and field-based research.

MOVING THE IDH FROM PATTERN TO PROCESS

What is a mechanism? Biological or theoretical framework?

From a theoretical point of view, two main mechanisms operate through environmental variability, and are consis-

Table 1 (a) Observational and (b) experimental studies in which intermediate disturbance hypothesis (IDH) patterns have been found

Source	Community type	Disturbance type	Aspect of disturbance intermediacy	Scale	Number of disturbance treatments observed	Range of disturbances studied
(a) Observational						
Aronson & Precht (1995)	Coral species	Storm generated debris	Integrated measure of disturbance: topographic complexity (more complex = less disturbed)	Landscape scale (>10⁴ m²)	Continuous	Topographic complexity from c. 0.2 to 0.8 days
English & Bowers (1994)	Old fields	Burrowing woodchucks	Intermediate distance from woodchuck burrows (frequency of visits)	Field	6	Distance from burrows of 0–16 m
Fox (1981)	Alpine plants	Soil disturbance by frost action	Extent	Field	Continuous	From 0 to 88% disturbance
Guo (1996)	Desert plant communities	Burrowing bannertail kangaroo rats	Intermediate distance from bannertail kangaroo rat burrows (frequency of visits)	20 ha	5	0–10 m from mounds
Hiura (1995)	Japanese beech forests	Gaps (caused by windstorms)	Extent (did not support IDH), frequency (supported IDH); temperature was more important in explaining diversity	Geographic (23 forests)	Continuous (estimated from published records)	Windstorm intervals between 2 and 14 years
Martinsen et al. (1990)	Shortgrass prairie plants	Burrowing pocket gophers	Intensity, time since disturbance	Field/ranch scale	3	<10% open habitat to >75% open habitat
Miyake & Nakano (2002)	Stream invertebrates	Deposition and erosion	Intensity	Two scales: reach (did support IDH) and patch (did not support IDH)	3	Many different measures
Molino & Sabatier (2001)	Tropical rain forests	Light gaps in canopy (tree fall, logging or poisoning)	Unclear; % heliophilic/pioneer stems used as a measure of disturbance	Landscape scale	Continuous	0–80% pioneers/heliophilic
Sheil (2001) (using Eggeling's data)	Rain forest	Poisoning of non-commercial tree species	Time since disturbance	Field	Unclear	60-year period observed
Stone & Wolfe (1996)	Lodgepole pine understory vegetation	Pine beetle epidemic induced tree mortality	Intensity	40 1 ha plots	Continuous	Per cent mortality from 5 to 94%

Table 1 *continued*

Source	Community type	Disturbance type	Aspect of disturbance intermediacy	Scale	Number of disturbance treatments observed	Range of disturbances studied
Suren & Duncan (1999)	Bryophytes in streams	Variation in stream flow (discharge and flood frequency)	Frequency, intensity	40 m transects in 48 streams	Continuous	Looked at several disturbance measures
Szentkirályi & Kozár (1991)	Apple insect communities	Management (insecticides, adjacent vegetation)	Intensity	Multiple fields	5	Abandoned – intensely managed orchards
Townsend et al. (1997)	Stream macroinvertebrates	Stream bed movement during high water discharge	Frequency, intensity	54 stream sites in seven river subcatchments	Continuous	Frequency from 0 to 1, log intensity from 1 to 2
Vetaas (1997)	Oak forest	Tree lopping	Intensity	Mountain	6	Slightly to very disturbed
Vujnovic et al. (2002)	Grassland remnants	Grazing	Intensity	Several fields	5	None to topsoil eroded
Willby et al. (2001)	Standing crop in canals	Boat traffic	Frequency	331 widely distributed sections of channel	Continuous	Low to high traffic density
Zacharias & Roff (2001)	Marine organisms on intertidal rockbeds	Wave damage	Extent	180 coastal sites	Continuous	Fetch from 0 to 200 km
(b) Experimental Austen et al. (1998)	Meiobenthic nematode	Macroinvertebrate predation and physical disturbance of sediment	Intensity	Mesocosm	7	Species at low, medium and high densities (separately)
Bowers (1993)	Old field plants	Mammal herbivory	Intensity	Field	4	No disturbance to multispecies predation
Buckling et al. (2000)	Genetic strains of a bacterium	Non-specific mass mortality events: 99.9% culture discarded	Frequency	Microcosm	5	0 – daily for 16 days
Collins et al. (1995)	Tallgrass prairie	Fire	Frequency (did not support IDH), time since disturbance (did support IDH)	Field	4	1–20-year intervals

Reference	System	Disturbance	Type	Setting	No.	Range
Floder & Sommer (1999)	Plankton	Mixing of vertical lake stratification	Frequency	Field	6	2–12 days
Hacker & Bertness (1999)	Salt marsh	Tidal flooding	Intensity/duration (position in intertidal)	Field	3	Low, upper middle and lower middle intertidal zones
Hixon & Brostoff (1983)	Algal substrates within damselfish territories	Grazing by damselfish	Intensity	Field	3	No grazing to intense grazing
Lubchenco (1978)	Intertidal tide pools	Grazing by herbivorous marine snail	Intensity	Field	6	0–250 snails m^{-2}
McGuinness (1987)	Intertidal communities under boulders	Waves overturning rocks	Frequency (determined by size of rock)	Field	5; 3	20–491 cm^2 rocks; fully buried to unburied
Schratzberger & Warwick (1998)	Nematode communities in mud	Physical disturbance	Frequency	Microcosm	7	No disturbance to disturbed continuously for 57 days
Sommer (1995)	Marine phytoplankton	Removal of part of population and addition of fresh nutrients	Frequency, intensity	Microcosm	5	0–14-day intervals
Sousa (1979a,b)	Algae on intertidal zone boulders	Storm-induced movement of boulders	Frequency (confounded with extent as smaller boulders are disturbed more often)	Beach	Continuous	Several experiments
Thorp & Cothran (1984)	Benthic macroinvertebrates	Predation by dragonflies	Intensity	Field microcosm	4	0–8 dragonflies
Weider (1992)	*Daphnia* clones	Dilution of microcosm	Frequency (supported IDH), intensity (did not support IDH)	Microcosm	4 Frequency; 4 intensity	0–21 day period; dilution volumes of 0–1900 mL
Widdicombe & Austen (1998)	Benthic macrofauna	Grazing by heart urchin	Intensity	Mesocosm	3	0–71 urchins per m^2
Wilson & Tilman (2002)	Old field	Tilling	Intensity	Field	4	0–100% bare ground

Table 2 Theoretical studies of the intermediate disturbance hypothesis (IDH)

Source	Community type	Disturbance type	Aspect of disturbance intermediacy	Number of species	Comments
Barradas et al. (1996)	Not specified	Not specified	Frequency	2	
Caswell & Etter (1999)	Not specified	Not specified	Frequency	2	Facilitation, tolerance, inhibition models
Dial & Roughgarden (1998)	Marine organisms with complex life cycles (e.g. barnacles)	Disturbance affects adult mortality	Intensity	2	
Elliott et al. (2001)	Phytoplankton	Mixing	Frequency, duration	8	Duration is called intensity
Kondoh (2001)	Not specified	Not specified	Not specified	Many	Explores productivity–disturbance–diversity
Lavorel et al. (1994), Lavorel & Chesson (1995)	Annual plants	Local disturbances (e.g. frost heaving, digging or trampling by animals)	Frequency, extent	2	Discussion of underlying mechanisms, including storage effect, operating in this system
Levin & Paine (1974)	Rocky intertidal zone (but applicable to other systems)	Waves, logs, etc.	Time since disturbance, extent	Many	
Moen & Collins (1996)	Plant communities (with herbivores and predators modelled explicitly)	Grazing/predation	Intensity	Many	Multiple trophic levels
Roxburgh et al. (2004)	Plants (but applicable to other systems)	Not specified	Frequency, extent	Two species, many species	
Savage et al. (2000)	Forest	Lightning generated fires	Frequency (which affects intensity)	Many	
Wiegand et al. (1997)	Shrub plants	Aardvarks, foxes, man	Frequency, extent	Many	Extent had no effect
Wootton (1998)	Non-specific food webs	Not specified	Not specified	Many	IDH supported for basal species under some conditions, especially when disturbance impacted one trophic level only

tent with the IDH (although traditional fluctuation-independent mechanisms may also be operating). These are termed 'the storage effect' and 'relative nonlinearity' (Fig. 2, Chesson 1994, 2000b; Roxburgh et al. 2004). The *storage effect* acts when there is sub-additivity in a species (usually the poorer competitor's) response to competition in good and poor environments. This response is reflected at the population level through the presence of buffering mechanisms (e.g. seed banks, diapause), which allow the species to store (hence the name) resources during times of relative harshness and yet re-emerge in the population at other times. Figure 2a illustrates how the population growth rate in good and poor environments reflects the storage effect. Note that additivity (curves parallel) is a neutral situation, while superadditivity (the curves diverge as competition increases) promotes extinction of the species. *Relative*
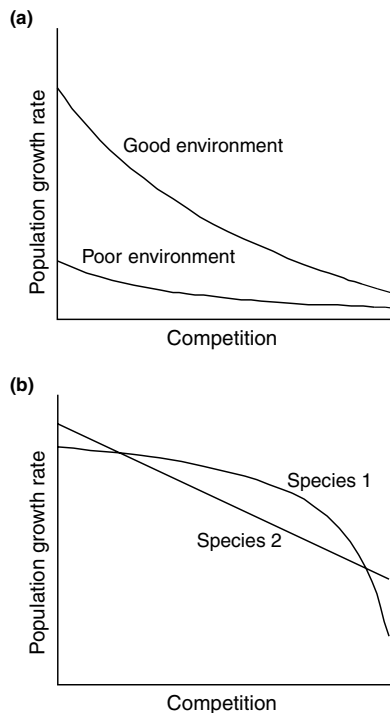
Figure 2 Curves illustrating the key features of the two main fluctuation-dependent mechanisms of species coexistence (redrawn from Chesson 1991). (a) Sub-additive growth in the poorer competitor is the main characteristic of the storage effect mechanism of coexistence. It can be detected by plotting population growth rate against the degree of competition experienced in two contrasting environments ('poor' and 'good'). (b) The relative nonlinearity of the responses of two competitors to competition, as illustrated in this figure, constitutes an alternative mechanism of coexistence.

nonlinearity acts when the population growth rates of competing species respond differently and nonlinearly to competition (or resource availability) – for example, if one responds linearly to increasing competition while the other responds in a nonlinear fashion and is affected very badly by high competition. The *storage effect* and *relative nonlinearity* constitute different 'mechanisms', because the attributes of the system required to generate coexistence are distinct in each case.

A potential difficulty in applying these theoretical ideas is that different biological attributes may have an equivalent mathematical basis, and hence may be expressing the same underlying theoretical mechanism. For example, a component of coexistence under the IDH may depend in one case on the presence of a seed bank and in another case on the reproductive longevity of a masting tree. In both cases the underlying theoretical coexistence can be generated by the same mathematical formulation; the storage

effect (Chesson 1994, 2000a; Roxburgh *et al.* 2004). The fact that a variety of biological characteristics can be represented in identical mathematical terms shows the strength of adopting a mathematical definition of mechanism, with the theory able to capture a range of phenomena in a general way. However, it also highlights the care that must be taken when attempting to relate the biological attributes of species to potential underlying coexistence mechanisms. For this reason we reserve the term 'mechanism' to differentiate fundamentally different theoretical bases for coexistence, whilst at the same time appreciating that the components of these mechanisms intimately involve the many and varied ways in which species can differ.

Note that the original IDH was couched in terms of a competition-colonization trade-off, but colonization can arise from either dispersal in space (e.g. spatial movement of dispersive life stages or from outside the disturbed area) or in time (e.g. germination from a seed bank). In the former, patchy disturbances are a requirement for coexistence; in the latter, disturbance can be 'global', in the sense that all individuals are affected by the disturbance, with the key components of the coexistence mechanism occurring within the disturbed area. Both biological situations have been shown to generate classic IDH patterns in models, but the underlying theoretical mechanisms may differ (Roxburgh *et al.* 2004).

Differentiating between different mechanisms

Central to moving the emphasis of IDH studies from quantifying pattern to understanding process is the ability to identify what attributes of the system are contributing to coexistence, and to identify what coexistence mechanisms are operating. The first step demands a study of both the nature of disturbance, and investigation into how the component species are responding. Key information includes various attributes of the disturbance regime, and knowledge of the species life history attributes.

In Roxburgh *et al.* (2004), identification of mechanism was made possible by searching for characteristic 'signatures' of relative nonlinearities and the storage effect within the models (Fig. 2). In short, different scenarios can generate the same outcome (coexistence at intermediate disturbance regimes), yet underlying that coexistence can be different mechanisms. These can be detected by quantifying (1) the growth rates of the different populations through time, and (2) the strength of competition that the species are experiencing. The latter may be either a direct measure of competition such as density-dependent decline in population growth rate, but may also be measured by quantifying the resources for which species are competing. This information can be displayed in the form shown in Fig. 2

to differentiate between these two mechanisms (see Fig. 3 of Roxburgh *et al.* 2004). In the final section of this paper we attempt to extend this approach, and propose an analogous methodology for identifying mechanism in field-based and experimental research.

INTERMEDIACY OF DISTURBANCE AND SPECIES COEXISTENCE

When is the IDH expected to operate?

There are a number of implicit requirements for the IDH to operate. First, obviously, *disturbance* must occur in the system. Second, *competition* must be operating within the community, such that in the absence of disturbance the competitive exclusion of weaker competitors is inevitable (Chesson & Huntly 1997). Finally, disturbance must result in a re-setting of the successional process. Importantly, if there is no predictable *successional* sequence of species in a community for disturbance to interrupt, then the 'reset-ting the clock' aspect of the process does not exist. Chesson & Huntly (1997) have demonstrated for species coexistence under the IDH the importance of the components of disturbance, a competition-driven succes-sional process, and the ability of the species to differentiate themselves in some way to the resulting spatio-temporal variability, i.e. to exhibit spatio-temporal niche differentiation.

Types of disturbance

Disturbances can differ in several key ways. For a given type of disturbance, for example, a flood, the disturbance frequency, intensity, extent and duration are all important characteristics.

Frequency of disturbance addresses how often a dis-turbance event occurs – it is the reciprocal of time between disturbances, which maps to another commonly used measure: *time since last disturbance*. *Extent* relates to the area affected by the disturbance. *Intensity* (or severity) pertains to the vigour of the disturbing force. *Duration*, which is less commonly considered, describes how long an individual disturbance lasts.

Disturbance: separating cause, effect and response

It is easy to confuse the cause of a disturbance with its effect on the species in the disturbed location and their resultant response, but it is important to distinguish all three of these aspects. For example, a species suffers 50% mortality (the effect) from a fire (the cause). In response to the subsequent opening up of space from the disturbance, a flush of seedlings germinate (the response). The same fire may kill

some species yet have negligible effect on others. And, even if the effect on two species is the same, the observed responses may differ (e.g. seedlings may germinate in one species while the other responds with clonal growth).

Quantification of the disturbance (e.g. wind speed, fire temperature, flood depth, duration and extent) provides a common measure that unites the differential effects and responses of the species in the disturbed area. A hot fire may result in the death of all biomass in the burned area, while a cool fire may remove litter and some vegetation, but leave trees and shrubs more or less intact. However, it is the effect and response to the disturbance that are important in defining species behaviours, and hence provide the key ingredients for a coexistence mechanism. The response to intense grazing (initiation of germination) might be different to the response to mild grazing (stimulation of flowering/ seed set), with each response maintaining diversity in a different way. In that sense, the way in which the disturbance regime scales with the life history of the species disturbed is a critical aspect. It is only when we examine the disturbed species that we can begin to define 'intermediate', the topic of the next section.

Defining intermediacy: issues of temporal and spatial scale

The word 'intermediate' is subjective, and we are not the first to point out that there is a need for operational definitions of intermediacy (Huston 1994). In particular, intermediate is often defined in terms of the conditions under which diversity is maximized – a circular argument, and a relatively unhelpful one for predictive purposes (Huston 1994). Instead, intermediacy must be defined based on species life history characteristics, as it is the response of the species to disturbance that generates the pattern (Moloney & Levin 1996). All the species in the community, and the way in which they interact, may also play a role in that definition.

Frequency
Frequency of disturbance must be scaled in part on the generation time of the organisms in the community (e.g. Padisak 1994). For mortality inducing disturbances, the shortest generation time provides a lower bound by which to scale intermediacy. If disturbances occur so often that even individuals of the shortest-lived species cannot reproduce, then we are left with our minimum possible biodiversity of zero species. An upper bound to an intermediate regime is provided by the rate of competitive exclusion of other species in the community by the competitive dominant, or by the time to climax community in a successional sequence (Reynolds 1993). An intermediate frequency disturbance regime therefore lies between the generation time of the shortest-lived species, and the time to

exclusion of other species by the most competitive. As the latter component depends on the attributes of all the species in the community, this must be defined specifically for the system in question, with the subsequent conclusion that 'intermediate' will also be context dependent.

Time since disturbance is often used as a measure of interest in spatially patchy landscapes. Here the assumption is that succession proceeds equivalently in all patches, so that studies of different areas which were disturbed at different times directly map to frequency information: such assumptions may be false (Clark 1989) and may explain the inconsistent frequency and time since disturbance results of Collins *et al.* (1995). Note the need for spatially limited (i.e. patchy) disturbances in this case – a global disturbance (which affects all organisms within the community, regardless of their spatial locations) would not offer this opportunity to juxtapose space and time.

Extent
Intermediacy in the extent of the disturbance must also be defined based on characteristics of the species in the community. Competition-colonization trade-offs are often cited in such circumstances. Here the distance which individuals can disperse or move provides a suitable measure of extent. However, in cases where there are no differences among species in their dispersal abilities, or where underlying mechanisms do not involve a spatial component, e.g. if dispersal occurs through time (seed banks or diapausing organisms or other storage stages) then even a global disturbance may permit a version of the IDH to operate (Roxburgh *et al.* 2004), and spatial extent is less relevant.

Intensity
Intensity or severity has two components. First there is the intensity of the disturbance itself, and then there is the effect on the species in the community. For the IDH, it seems important to quantify the former, but it is the effect that affects mechanism. The intensity of the disturbance itself is a common currency that applies to all the species in the system and gives a single axis on which to measure the disturbance. For example, Gignoux *et al.* (1997) measured fire intensity by using thermo-sensitive markers which showed an irreversible colour change at different temperatures to infer the maximum fire temperature. However, the same intensity of disturbance will map to different effects on different species. Intensity of effect can be scaled from no effect to mortality of an organism, with a range of morbidity effects in between (different degrees of biomass loss and loss of regenerative or reproductive tissue; see e.g. Klimešová & Klimeš 2003). Different life history stages may also be differentially affected. For example, green plant matter may be destroyed by fire while seeds remain

unharmed; diapausing individuals survive droughts while their non-diapausing counterparts do not.

Duration
Duration is less commonly addressed in IDH studies, and is sometimes considered as an aspect of intensity (e.g. Elliott *et al.* 2001) or is specifically excluded from consideration by requiring disturbances to be relatively instantaneous (e.g. Petraitis *et al.* 1989; Mackey & Currie 2001). However, the distinction between how long a perturbation lasts (units of time) and how severe it is (units of temperature or wind speed or water depth or some sort of amount) is important. Press (sustained) and pulse (relatively instantaneous) perturbations certainly differ in their effects (Bender *et al.* 1984). Where does 'intermediate' lie on the continuum between press and pulse perturbations? Duration, like frequency, may be defined relative to the life cycle of the organisms involved, but also, like intensity, to their tolerances for the disturbance characteristics. For example, organisms trapped by floods for a short time may survive and recover, but eventually they would die, if not of drowning, of starvation or other effects of the inundation. The response of communities to press disturbances, for example, the gradual increase in atmospheric CO_2, is relatively little studied. It is possible that communities will adapt to the changing conditions, with correspondingly gradual changes to structure and function. However, there is also the potential that they might initially respond gradually to a press disturbance, but at some critical point collapse and form a completely new system.

Interactions between disturbance attributes
An overarching issue is the nature of interactions between these attributes (Sousa 1985; McCabe & Gotelli 2000). A species response may depend on the frequency, intensity, extent and duration of a disturbance to differing degrees, but all are linked. For example, individuals may be able to tolerate very frequent disturbances if they are of low intensity, or fairly intense disturbances if they are of short duration. At certain observational scales, one attribute may dominate (Collins *et al.* 1995; Vandermeer *et al.* 2000). Their interaction also provides spatio-temporal niches by which different species are distinguished and hence can coexist. For example, two species may respond similarly to short disturbances at a range of frequencies, but very differently over the same range of frequencies if the duration is longer. Only in the latter case might IDH mechanisms generate coexistence. Indeed, it is the presence of spatio-temporal niches, resulting from variability in environmental conditions resulting from repeated disturbance that hold the key for understanding species coexistence under the IDH.

Certainly there are operational issues that arise when considering multiple attributes. Is the IDHs focus on intermediacy applicable to all four ways in which disturbances differ? By far the most commonly studied are intermediate frequency and intensity disturbances, but research exists supporting the IDH for all these attributes. Similarly, for disturbances of differing durations, how should intensity be measured? Possibilities include measuring the mean or maximal intensity, or the time-integral of all the instantaneous intensities. The potential for within-disturbance variability and nonlinearities is interesting. A week of low-intensity fire, with 1 day of severe fire, would likely produce quite different effects than a week of fire at the mean intensity.

Petraitis et al. (1989) combine different measures of disturbance attributes into a single measure (e.g. the product of extent and frequency, which they term intensity, not to be confused with our definition of the word). This may prove useful in summaries, but averages over possible nonlinearities (Petraitis et al. 1989), which may conceal important mechanisms.

SURVEY OF OBSERVATIONAL, EXPERIMENTAL AND THEORETICAL STUDIES

Given the recent theoretical insight that coexistence under the IDH can arise from a number of different coexistence-promoting mechanisms, and given the above discussion of the wide range of attributes related to disturbance and their effects on species, we asked how well the current literature can inform us about these various issues.

We surveyed over 250 papers, reviews, book chapters and books that discussed or directly addressed the IDH themes. As well as standard works, articles were found in searches of databases (Current Contents and Web of Science) and of references listed in all relevant studies. However, this search was not meant to be exhaustive; the intention was to highlight some of the contexts in which the IDH has been shown and what has arisen from that research. Of these, many studies just mentioned the IDH; most of those deleted were observational. Others found little or no evidence for the operation of an IDH mechanism in the system of interest – such papers were also excluded as beyond the scope of this study (for a comparison of the frequencies with which different relationships between diversity and disturbance have been supported see Mackey & Currie 2001).

Within the review we found a slew of obvious common problems. Of the >250 papers initially considered, a surprisingly large number of studies discuss the IDH in the context of a single species, or with only two levels of disturbance. Some studies of single species have suggested that higher abundances at intermediate disturbance levels are related to the IDH, but the IDH makes no claims about abundances and in fact at higher species diversity abundances of the species present may be lower as more species compete for the same resources. Other studies compare species diversity at different times of year and so do not control for seasonal variation. As the IDH refers to two or more species coexisting with a pattern that is predicted to be nonlinear, it is necessary to span a broad range of disturbance attributes (frequency, etc.) to be confident that a pattern could be observed (Grime 1973a; Martinsen et al. 1990; Vujnovic et al. 2002). For example, studies might find only a monotonically increasing (Fig. 1, points A, B, C) or decreasing (Fig. 1, points C, D, E) pattern, possibly no effect (if the peak is not sharp, Fig. 1, points B, C, D) or a plateau (e.g. Fig. 1, points A, B, D) if inappropriately situated. Even if a full range of disturbances is covered, experiments may be designed with insufficient statistical power to detect such patterns, particularly if there is unexpectedly high variation (see the discussions in Beckage & Stout 2000; Huxham et al. 2000). How often, how intensively and over how wide an area species diversity is sampled affects measured outcomes (Mackey & Currie 2001). IDH patterns are more commonly found in studies of sessile organisms than of mobile organisms (Mackey & Currie 2001). This may relate to spatial scale of the observations made; mobile organisms can also respond to disturbance by moving and this may make a pattern harder to observe for a given set of conditions (Sousa 1984).

We here present two tables highlighting relatively recent studies that give support to the IDH. Table 1 shows a summary of observational ($n = 17$) and experimental ($n = 16$) studies, while Table 2 describes theoretical/modelling studies ($n = 12$). Note that we have interpreted the studies as best we can, based on information provided in the published papers only. Because some authors were investigating related concepts (but not specifically IDH) or other aspects of IDH than we were examining, it was not always obvious how to categorize some studies. In particular, sometimes which aspects of intermediacy (frequency, etc.) are being considered is unclear.

The IDH has been supported in a huge range of community types (from aquatic to terrestrial) at scales ranging from microcosms to the entire landscape (Table 1). Experimental work tended to be carried out at smaller spatial scales than observational studies, presumably for tractability reasons. Theoretical studies tended to be very general in scope, although some were targeted at specific natural systems (Table 2). Interestingly, most empirical studies focused on primary producers or basal species, or on sessile organisms. This may be because the species are more likely to be competing for the same resources, and almost certainly because organisms that cannot move are more easily studied in a disturbance context (Sousa 1984).

Two models attempted to look at the multitrophic implications of IDH (Moen & Collins 1996; Wootton 1998).

Disturbances also are very varied and include natural disturbances such as storms, predation, water flow changes and floods, fire, as well directly human-mediated disturbances such as tilling, boat traffic and dilution (in microcosms). The number of disturbance categories varied considerably. Often there were three levels (low, intermediate, high); other studies looked at a continuous gradient of disturbances. We focused on studies which contained at least three levels of disturbance, in order to allow characterization of intermediacy. The range of disturbances was often quite large [from 0 to 100% ground cover disturbed (Wilson & Tilman 2002) or 5 to 94% mass mortality (Stone & Wolfe 1996)]. Some data were from studies lasting a few weeks while others were from long-term data sets (e.g. Sheil 2001 used a 60-year data set).

In empirical studies intermediacy was defined in terms of intensity (17 cases), frequency (13 cases), time since disturbance (three cases), extent (two cases), and duration (one case) although sometimes the attribute measured was unclear. Theoretical studies focused more heavily on frequency (seven cases), but extent (four cases) and intensity (two cases), time since disturbance (one case) and duration (one case) also were considered. Despite the fact that duration of disturbance is an important component of many systems, it was never explicitly, only implicitly, addressed. Similarly, relatively few studies addressed multiple aspects of disturbance (see Tables 1 and 2 for exceptions), and it was not always clear that excluded aspects were controlled. This is in part due to the fact that in observational studies, which examine the effects of 'natural' disturbance rather than creating disturbance as an experimental treatment, it is often difficult to categorize the nature of disturbance – natural disturbances tend to vary on more than one axis simultaneously.

Most natural system studies examined the IDH in terms of maximizing diversity (species richness or some other measure of diversity). Two microcosm studies examined genetic diversity within a single species (Weider 1992; Buckling et al. 2000), and one field study focused on the presence of four target species (Hacker & Bertness 1999). Theoretical studies had a more even split between multispecies and two species approaches to coexistence under IDH. Roxburgh et al. (2004) show how their two-species conclusions can be extended to multiple species.

We conducted this survey in part with the hope of elucidating underlying mechanisms involved in different systems. However, we found this nearly impossible to do with the information usually presented in papers. We have analysed a few empirical studies and models in greater detail and associated them with likely underlying mechanisms (Roxburgh et al. 2004), but the overwhelming number of studies did not provide information that would allow us,

even tentatively, to identify the underlying coexistence mechanism or its components. In part this is because many were focussed on merely quantifying the pattern of higher diversity at intermediate disturbance. Confirming that the IDH is indeed real, and occurs across a range of systems, is of course the important first step towards understanding it. However, this review highlights that the time is ripe to move to the next level, and to begin asking just how the IDH operates, over and above determining its presence.

The review also provided some tantalizing glimpses of exciting new avenues for research. These are discussed below.

Interactions between disturbance types

In some ecological systems more than one type of disturbance may be operating (Hobbs & Huenneke 1992). In the few studies of such interactions, it has been shown that disturbance history matters. For example, Fukami (2001) alternated drought and larval mosquito addition disturbances in a variety of sequences in laboratory microcosms and found that the diversity outcomes differed. Similarly, Platt et al. (2002) found that the effects of hurricanes depended on prior fire regimes in Florida. To our knowledge, no work has directly assessed whether the IDH applies in such interactions, however, the importance of such studies will increase in the face of global climate change. Certainly, such press disturbances will interact with existing pulse disturbance regimes.

Operation of the IDH in multi-trophic systems

Most of the IDH studies we have identified and discussed involve primary producers (although sometimes the disturbing agent is at a different trophic level). However, there are two recent modelling studies that examine the effects of the phenomenon in multi-trophic systems. Models of one, two and three trophic layers of different composition found cases where hump-shaped diversity–disturbance relationships (as in the IDH) were observed (Moen & Collins 1996; Wootton 1998). Interestingly, these patterns were more common in basal species. However, there were also cases where the IDH pattern was not observed. Further exploration of this issue in model and empirical systems is warranted.

Interactions between productivity and diversity under disturbance

Because a major defining property of disturbance is the release of resources for other organisms to exploit, an interesting side issue is how the overall levels of resource in a system modify the interactions between species in a

community undergoing a given disturbance regime. Models by Kondoh (2001) suggest that the peak of the diversity–disturbance curve moves in response to increased productivity. Wilson & Tilman (2002) found empirically that overall species richness in an old field decreased with increasing nitrogen levels at all disturbance levels – humped curves were only seen at the lowest nitrogen levels. Similar results have been recorded for plankton (Beisner 2001).

Changes in disturbance regimes

While the impacts wrought by disturbances are difficult to study, this is even more true of changes in disturbance regimes. Mack & D'Antonio (1998) reviewed the effects of invasive species on existing disturbance regimes, as well as cases where such species triggered new disturbance regimes. Such shifts are likely to dramatically affect diversity, and can also be initiated by direct human interference (as in the fire regimes in California and Australia) or by elements of global climate change. In a similar vein, Moloney & Levin (1996) addressed the impact of changes in the spatio-temporal correlation structure of a model disturbance regime. Different underlying mechanisms might generate different responses to such changes; understanding the possible outcomes is essential if we are to ameliorate possible impacts on global biodiversity.

Evolution under disturbance and changing disturbance regimes

The historical disturbance regime has shaped species response to disturbance. Thus, disturbance regimes may be 'expected' by the species in the community if they are adapted to that particular disturbance regime (Sousa 1984). However, all species live in variable environments and it is important to distinguish between the expected and the unexpected. Seasonal variation is within the normal range of experience of many organisms, but an unusually severe or early winter might constitute a disturbance in this context. Similarly, in fire-adapted communities, a *change* in the frequency or intensity of fires, rather than a single fire, would constitute a disturbance (Mack & D'Antonio 1998). The change in the regime leads to a change in the way the species are affected, or are able to respond, particularly in relation to their temporal dynamics (age to maturity, etc.). For press disturbances, the speed with which the perturbation is applied is also important. If an extreme disturbance occurs abruptly, for example, anthropogenically forced global temperature increases, the effect may be very different than if it occurs more slowly – certainly adaptation is more likely in the latter case.

Given the importance of the interactions of the disturbance regime with life histories of the species involved, linking observational, experimental and modelling studies of the same system would be particularly informative. Thus, we outline below an approach to designing an integrative IDH study, with attention to generating a deeper understanding of the underlying mechanisms.

DESIGNING AN IDH STUDY: LINKING OBSERVATIONS, EXPERIMENTS AND THEORY

Is the IDH a coexistence-promoting mechanism in my system? This main question encompasses two subsidiary questions: Does the unimodal diversity pattern exist? and, if so, what mechanisms generate this pattern? Our approach to answering these questions would involve coupling observational, experimental and theoretical/modelling studies in a multi-pronged attack. Here we describe a hypothetical research agenda for grazing disturbance effects on species diversity in a pasture community. The purpose of the example is not to prescribe a specific research plan for a particular situation, but rather, to highlight the range of questions that should be considered when designing a field experiment that seeks to both quantify the IDH, and to gain a deeper understanding of the underlying mechanisms responsible for that pattern.

Studies of old fields (e.g. Tilman 1987) certainly suggest a competition-driven successional process operates in field systems. Thus we have our prerequisite of a directional sequence of species composition. It appears likely that disturbance in the form of grazing would interrupt this process by removing vegetation from the system. Initial observational studies might examine species diversity in a series of pastures and correlate diversity with known grazing histories. Such information could also be gleaned from previous studies with other aims. This would help to highlight relevant spatial and temporal scales to examine, and other pertinent aspects to explore: basically to set the scope of the study. Examination of associated theoretical work, combined with development of simple models of the main pasture components (e.g. annual and perennial grasses, legumes and broad-leafed weeds) and the effects of and their responses to different grazing pressures would occur concurrently. Together these would be used to design an experiment (or suite of experiments) to address the aspects (frequency, intensity, etc.) of the disturbance and their interactions. Without the benefit of this background research we present a possible design to illustrate the process. Note that initially we assume ample time and resources for this study – obviously constraints on these factors would involve some compromises in experimental design and consideration of the optimal distribution of effort given the question (Crawley 2002). Significant resource constraints also underlie the increasing appeal of microcosm studies (Buckling *et al.* 2000).

Frequency

The shortest lived species will be annuals, suggesting an annually applied grazing pressure is appropriate. If we assume the climax community is reached after *c.* 60 years (e.g. as suggested by Inouye *et al.* 1987) the longest period between grazing might be 60 years or even 120 (if you have LTR funding!). In between would lie a variety of shorter disturbance frequencies: every 2, 5, 10, 15, 20, 30 years, for example.

Extent

The area required for a single grazer would probably determine the size of the smallest experimental units in this example. Observational studies of dispersal of the most common species would suggest the largest scales of interest. Given that many pasture species are wind dispersed, the long distances involved suggest an exploration of spatial extent is less interesting for this system as few species are likely to be limited in their ability to reach the sampling areas in even a very large disturbed area.

Duration

Livestock might be pastured on the experimental units for one, two or three seasons a year (spring, summer, autumn) to span the range from pulse to press disturbances. Note that this combination of the duration and frequency timescales raises the issue of which one or two seasons should be grazed each year, an additional factor that can be included in such seasonal systems if of interest. The exact timing of equal duration grazing events is likely to be important (the effect of grazing during spring germination might be very different than the same grazing pressure applied during autumn flowering).

Intensity

Cattle stocking rates (number of cattle per unit area) could be varied from very low grazing pressures to crash-grazing levels (where stocks are so high that nearly all vegetation is devoured during the stocking period). Note that it is possible to arrange different duration and intensity schedules that generate the same number of 'cow days' per plot per year. In this way duration and intensity can be considered to be related. However, while the application of the disturbance may appear equivalent, the effect may be very different. One cow in a plot for 30 days allows time for some vegetation to regenerate, 30 cows in the same area for 1 day (crash grazing) does not, and less-favoured plants are far more likely to be eaten in the latter scenario. The effects of the different grazing regimes on the size, growth, reproduction and survivorship of the pasture species should also be quantified – the response to grazing may not vary linearly even if the grazing pressure does.

Measures of diversity

While the classic IDH was couched in terms of number of species, and some researchers are adamant that species number is the only appropriate measure (Sommer 1995), other researchers have used measures of biodiversity other than species richness, for example, measures that incorporate abundance (Lubchenco 1978) or functional diversity measures (Willby *et al.* 2001; Weithoff 2003). A review of the different measures of diversity that have been used in the study of diversity–disturbance relationships is given by Mackey & Currie (2001). In easily accessible systems of sessile organisms several methods can be used and compared; in less tractable systems more concern with diversity sampling protocols and their interpretation in the context of the IDH is necessary. The measure of disturbance should be independent of the measure of diversity to avoid circularity.

Efficient experimental design and scales of observation

As Fig. 1 suggests, one must have at least three treatment levels for each axis (frequency, intensity, extent, duration), spanned across a suitable range. If interactions between the four attributes are also to be explored in a full factorial design this generates $3^4 = 81$ experimental units, even before replication. Unless pilot and observation studies suggest a suitable arrangement of treatments, however, it will almost certainly be better to have more levels for each axis. If interactions with nutrient levels, or investigation of multiple disturbances are also of interest further treatment axes can, in principle, easily be included. Again, few researchers would have the resources for such a comprehensive study. If certain aspects are omitted, however, they must be controlled for. For example, studies of fire frequency may confound with intensity as litter build-up in longer periods between fires may exacerbate temperatures.

The scale at which observations are made relative to the disturbances applied is an important component of the experimental design. How often should you measure diversity in your system and what area should be sampled? How these issues are resolved will depend on the questions to be answered, but may affect interpretation if the response time to disturbance differs from the observation time. Observations taken at the frequency of the most frequent disturbances would seem appropriate.

Part of the issue of spatial scaling arises from the observation that it is not always clear whether the IDH is intended to apply to diversity within a patch or to diversity in

the larger landscape of both more-or-less recently disturbed patches (Collins *et al.* 1995). Certainly, where spatial aspects such as dispersal are involved, the surrounding matrix of vegetation plays a role in recolonization following disturbance (and will be different if the surrounding vegetation is woodland rather than additional pasture) and the boundaries of the 'system' are larger than they might be considered in a case where spatial aspects are of lesser concern. Deciding how sampling and disturbance areas should be scaled relative to one another will depend on the community of interest. In the present example, we would suggest sampling a fixed size area at the centre of any size of treatment plot. Operating at the landscape scale raises the problem of appropriate replication of large experimental units.

Is the IDH operating?

Operation of the IDH requires competition in the system, and a successional process. For what resources are the species competing? Is succession occurring? Do we observe the unimodal pattern of the IDH in our treatments? If so, is the species diversity observed under particular disturbance regimes true long-term coexistence, or just slow competitive exclusion (i.e. are the diversity patterns stable)?

Search for underlying mechanisms

Until recently the focus has been predominantly on exploring the disturbance–diversity pattern, with less consideration of the underlying mechanism(s) by which diversity is maintained. This is perhaps not surprising, given the difficulties in determining what biological attributes the species might be expected to have in order to provide the essential ingredients for coexistence, and then demonstrating, in the actual community, that such attributes are both present and active in promoting species coexistence. Quantification of the disturbance itself (i.e. grazing) is important, however, the effect (e.g. loss of biomass to grazing) and response (e.g. growth rate of individuals after grazing) is what will determine coexistence in the system.

Figure 2 provides a theoretical framework within which empirical results can be interpreted, and which has the potential to promote a more mechanistic understanding of the way in which coexistence is maintained under intermediate disturbance in real communities. This approach has already been successfully applied in theoretical studies of the IDH (Roxburgh *et al.* 2004). In Fig. 2a sub-additive growth is a central component of the storage effect mechanism of coexistence (Chesson & Huntly 1989). Demonstrating the presence of sub-additive growth therefore provides strong evidence that the storage effect

is operating. The first axis that requires quantification is the population growth rates of the component species. The first step towards constructing an analogous figure for our hypothetical example therefore requires collecting data on the changes in the number of individuals (or biomass) of the component species through time, from 'good' environments which occur soon after disturbance, where resources are freed up and competition is negligible, through to 'poor' environments where disturbance has not occurred for some time, competition has become more intense, and resources more limiting. The competition axis is less straightforward to quantify and in many field situations its measurement may pose significant practical difficulties. Conceptually, it can be measured indirectly through measuring the consumption of resources, or directly through field-based density manipulation experiments. Similarly, to investigate the presence of relative nonlinearity, a figure of the form of Fig. 2b could be constructed from a similar combination of experimental and observational data. Note that although the relationships in Fig. 2 summarize the overall system behaviour, knowledge of the attributes of the component species, particularly differences in life histories strategies, is critical for an ecological interpretation of the coexistence mechanism (Roxburgh *et al.* 2004).

One potential limitation of this approach is that most communities comprise multiple species, yet Fig. 2a,b is based on the analysis of two-species systems. Similar patterns are expected in the multi-species case, however, the conditions for unambiguously determining the presence or absence of an active coexistence mechanism become more complicated. Nevertheless, observing patterns consistent to those in Fig. 2 would provide the first steps towards identifying the underlying coexistence mechanism.

An alternative approach, and one with perhaps greater analytical power, is to perform the kinds of experiments and analyses discussed above on artificial 'microcosm' communities, which may range from artificial mixtures of a manageable number of species established in containers/plots/exclosures within a natural field situation, through to microbial/plankton/growth chamber based studies, where even greater replication and control is possible, and where experimental costs are less prohibitive. This approach has already been successfully employed in the study of the IDH (Buckling *et al.* 2000), in studies of community assembly (e.g. Drake *et al.* 1996; Weatherby *et al.* 1998), and in the study of experimental evolution (e.g. Kassen 2002; Elena & Lenski 2003). It offers great potential for elucidating the mechanistic basis for coexistence under the IDH using real organisms, and provides a more tractable opportunity for making the necessary links between ecological theory and ecological application.

CONCLUSION

Two related themes have emerged from this review, which point to a way forward. First, combining both theoretical and empirical approaches will be necessary to simultaneously identify and test for the presence of coexistence-promoting mechanisms in real communities. This is because the theory is able to specify mathematically the mechanisms and their components, and therefore provide insight into what specific attributes of the natural system might require focused study. Reciprocally, the empirical work is able to inform the theoretical on the overall parameters of the system being studied, in addition to providing field validation of any theoretical predictions.

The second theme to emerge from this review is that the key to successfully integrating empirical and theoretical studies lies in having an adequate understanding of the species life history attributes (or more specifically, how these attributes differ between species). This is because life history differences differentiate the species in their response to the disturbance events, and therefore are key components in defining the spatio-temporal niches required for coexistence. In theoretical studies these differences in life history are usually clearly identified, either as model parameters, or explicit assumptions, or both (e.g. Lavorel & Chesson 1995; Moloney & Levin 1996; Roxburgh *et al.* 2004). Empirical studies, with a traditional focus on establishing the pattern, have been less focused on the attributes of individual species, and have usually adopted a broader perspective. Through combining the strengths of both approaches, we argue that significant advances could be made. Armed with these insights, a number of targeted questions can be asked to directly investigate the underlying coexistence mechanisms and their nature. For example, how do resources become available with disturbance, and are there shifts in which resources are limiting? What are the effects of the different disturbance components on the species in the system, and how do those species respond? How do the population growth rates vary with varying environmental conditions, and with resource availability? Are the effects and responses and their differences under different conditions consistent with theoretical predictions (i.e. sub-additive growth and buffering of population growth; or, relative nonlinearity in population growth rate with fluctuating resources)? Are other fluctuation-independent coexistence mechanisms present? Through asking such targeted questions, guided by the interaction between theory and empiricism, it is hoped that we will soon move beyond the mere documentation of the pattern, that the underlying processes will begin to be revealed, and that a deeper understanding of the role of disturbance in maintaining biodiversity in ecological systems will result.

Why is understanding processes underlying the IDH so important?

Most natural systems involve variation, whether that variation is within the normal range or not for the species involved. Thus fluctuation-dependent coexistence mechanisms are an important driver of global biodiversity and as such are of pure research interest. However, there is an applied motivation also. Disturbance regimes are changing drastically. Climate change (e.g. increased flooding and temperature extremes), biological invasions, and direct human modifications of the environment (e.g. dams) are either perturbing natural systems *de novo* or are modifying existing regimes. In the case of biological invasions generating or modifying disturbance regimes, such changes may generate a feedback loop if the new disturbance regimes favour additional new invaders more than the native community (Mack & D'Antonio 1998; Shea & Chesson 2002). Moreover, as species increasingly are moved (intentionally or not) as the result of human activities, their effective dispersal distances are greatly extended and the recolonization process that follows a disturbance takes on a very new complexion (Hobbs & Huenneke 1992). In order to predict and mitigate the results of such changes, we must understand how species diversity is likely to change as disturbance regimes change.

Such progress requires a rigorously defined research agenda, with the essential component of a clear insight into the mechanisms that might affect diversity in disturbed environments. A synthesis of theoretical and biological views is a necessary prerequisite. A major challenge remains the reconciliation of biological and mathematical mechanisms. On the biological side, the key will be to identify those life history and other traits that are required in order for a fluctuation-dependent mechanism to be expressed. From the theoretical side the key will be to use theory to identify aspects of the biologies of the species that are consistent with the action of different underlying mechanisms (Chesson & Huntly 1989), and then to explore those predictions empirically.

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