

Thesis for the degree of Doctor of Philosophy

Ecological disturbances:

The Good, the Bad and the Ugly

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ECOLOGICAL DISTURBANCES: THE GOOD, THE BAD AND THE UGLY.

Abstract. This thesis focuses on the definitions, characterizations and quantifications of ecological disturbances, as well as hypotheses on their impacts on biological communities. The most prominent model on effects of disturbance on diversity is the Intermediate Disturbance Hypothesis (IDH), which is utilized in management of national reserves, has received over 3300 citations and has been corroborated by a multitude of studies from terrestrial and aquatic systems. According to the predictions of the IDH, diversity is high at intermediate levels of disturbance due to coexistence of competitors and colonizers. At low levels of disturbance diversity will be low due to competitive exclusion and few species can persist at high levels of disturbance. In an extension of the IDH, the Dynamic Equilibrium Model (DEM) predicts that the effects of disturbance depend on the productivity of communities, because at high growth rates a stronger disturbance is required to counteract increased rates of competitive exclusion. The IDH and the DEM were tested in a field experiment on effects of physical disturbance (scraping) and productivity (nutrient availability) on hard-substratum assemblages in paper **I**, where the patterns predicted by the IDH, but not the DEM, were observed. This outcome shows the importance of the nature of productivity alterations, as the productivity treatment had a general positive effect on growth rates but only marginal effects on the dominant species, thereby leaving rates of competitive exclusion unaffected.

In paper **II** I tested another extension of the IDH, which predicts that smaller, more frequent disturbances will have different effects on diversity compared to larger, less frequent disturbances. In this experiment I used two different regimes of disturbance, small and frequent vs. large and infrequent disturbances, while the overall rate (the product of area and frequency) was kept equal for both regimes. At the site where the IDH was supported, the regime with a large proportion of the area disturbed infrequently showed higher richness, due to a stronger decrease of dominants, compared to the regime with a small proportion disturbed frequently. In addition to these significant differences in diversity effects between different disturbance regimes, it may also matter what agent of disturbance that is causing the damage. In paper **III** I contrasted the effects of a physical disturbance (wave-action) to that of a biological disturbance (grazing), as well as their respective interactions with productivity in a multifactorial design tested on natural epilithic assemblages. The composition of assemblages and the total species richness was significantly affected by physical disturbance and interactively by biological disturbance and productivity. The algal richness was significantly affected by productivity and biological disturbance, whereas the invertebrate richness was affected by physical disturbance. The results show, for the first time, that biological disturbance and physical disturbance interact differently with productivity due to differences in the distribution and selectivity among disturbances.

In paper **IV** I investigate how the choice of diversity measure may impact the outcomes of tests of the IDH, which, surprisingly, has not previously been discussed. This was done by an extensive literature review and meta-analysis on published papers as well as by two different approaches to mathematical modelling. Both models support the IDH when biodiversity is measured as species richness, but not evenness. The meta-analysis showed that two-thirds of the published studies in the survey present different results for different diversity measures. Hence, the choice of diversity measure is vital for the outcome of tests of the IDH and related models.

Key words: competitive exclusion; DEM; disturbance; diversity; evenness; IDH; marine assemblages; productivity; rate of disturbance; regime; species richness; Tjärnö, Sweden.

Populärvetenskaplig sammanfattning

Som den skamlöst fyndiga titeln syftar till så kan ekologiska störningar se väldigt olika ut och ha helt olika effekter på den biologiska mångfalden. Men innan vi ger oss i kast med en djupare tolkning av detta, bör vi bena ut vad en störning egentligen är. Exempel på vanliga störningar i naturen är skogsbränder, stormar, översvämningar, vågor, tråkning, föroreningar, uttorkning samt istäcken och drivved som skrapar bort arter på hårda bottenar. Lite ibland räknas även biologiska störningar, d.v.s. djur som tuggar i sig andra djur och växter, eller djur som i ren illvilja eller okunskap trampar ihjäl levande varelser i sin väg. För att krångla till detta en smula så får inte allting som kan ge upphov till skada kallas för en störning, utan i likhet med samhället i stort finns även här vissa som är mer jämlika än andra. Definitioner på vad som får räknas som en faktisk störning finns det lika många som antalet GAIS supportrar; ungefär nio. Enligt den mest konkreta och lätthanterliga definitionen ska en störning döda eller avlägsna organismer i ett samhälle (område med samexisterande arter), och därigenom underlätta för nya arter att etablera sig. Den till synes harmlösa bisatsen om etableringsmöjligheter får oanat stor betydelse när man testar ekologiska förklaringsmodeller om störning och biodiversitet.

Överlag sunda läsare undrar nu förmodligen vad i hela Hisingen en ekologisk förklaringsmodell är. Dessvärre kan jag inte skryta med att detta är lika komplicerat som det låter. En förklaringsmodell, eller hypotes, inom ekologi går helt sonika ut på att förklara ett fenomen eller samspel i naturen. I merparten av mina många experiment (tre) har jag undersökt om 'the Intermediate Disturbance Hypothesis' (IDH) verkligen stämmer. Denna hypotes går i princip ut på att 'Lagom är bäst' och passar därför väl in i den svenska kulturen. Anledning till att just lagom störning är bäst är att då finns flest antal arter, eftersom alla arter dör ut om det blir för mycket störning och att bara en art kommer ta över hela samhället om det inte finns någon störning alls. Det sistnämnda kallas 'konkurrensuteslutning' och innebär, kanske inte helt otippat, att en art kan konkurrera så effektivt att den utesluter alla andra arter ur ett område om ingenting stoppar den. Exempel på när detta sker i naturen är barrskogar och musselbankar, där en eller ett fåtal arter helt egoistiskt kan ta upp väldigt stora områden. Om en störning kommer in och dödar ett antal individer i dessa områden kan andra, nya, arter etablera sig på den nyligen frigjorda ytan eller marken. Antalet arter i området ökar då alltså, och är man lite fin i kanten kan man istället uttrycka detta som att den biologiska mångfalden höjts. En annan väldigt rolig hypotes, som bygger på den ovan nämnda IDH, kallas 'the Dynamic Equilibrium Model' (DEM). Tillägget i denna hypotes är att mängden störning som är lagom beror på hur fort arterna i ett samhälle växer. Desto fortare arterna växer, desto kraftigare störning krävs för att bryta konkurrensuteslutning av någon självupptagen liten gynnare. Dessa två hypoteser, IDH och DEM, är vad jag, två GAIS:are och ett gäng ohängda tyskar testat på marina hårbottensamhällen, bestående av anemoner, havsborstmaskar, havstulpaner, hydroider, musslor, mossdjur, svampdjur, sjöpungrar samt grön-, brun- och rödalger, i den första artikeln i avhandlingen.

De andra nagelbitarna till artiklar handlar även de om hypoteserna IDH och DEM, om än lite mer indirekt och med större fokus på själva störningsmekanismerna. Den näst första artikeln handlar om störningar som är lika stora i total omfattning, men där en störning som sker dubbelt så ofta då påverkar en hälften så stor yta. Skillnaden vi hittade här var att störning med stor yta som skedde mer sällan gav upphov till fler arter, eftersom detta mer effektivt

kunde bryta de slemmiga sjöpunngarnas konkurrensuteslutning. I det tredje experimentet slängde vi ett getöga på skillnaderna mellan samhällen på stenar som skrapar mot varandra i vågrörelser (fysisk störning), jämfört med samhällen på stenar som blir mumsade på av promiskuösa strandsnäckor (biologisk störning), samt vilken effekt dessa olika störningar får i samspel med hur fort samhällen tillväxer (produktivitet). Förutom att de olika typerna av störning interagerade på olika sätt med tillväxthastigheten, hade de även olika stor effekt djuren och växterna (algerna) i samhällena. Den fjärde och sista artikeln är mer lik en debattartikel, fast med stöd av matematisk modellering och en litteraturundersökning, där jag väldigt ödmjukt påstår att alla andra som jobbar med ekologiska störningar och biodiversitet gör fel, medan jag själv tvivelsutan gör allt rätt. Anledningen till felaktigheterna är att en del testar hypoteser om förändring i antal arter med ett mått på hur jämt arter är fördelade istället för hur många de är. Detta är lite som när Kurt Olsson frågade Patrik Sjöberg hur brett han har hoppat, eller som att räkna antalet äpplen i päronträd, makrillar i änglackleken eller marxister i vita huset.

Summan av kardemumman, efter ett halvt decennium på skattepengar och ett ointagligt rekord i spindelharpan, är alltså att effekterna av störning hänger på vilken slags störning som sker, hur man väljer att mäta den, samt vilka arter som finns i samhället där störningen inträffar. Vill man testa hypoteser om biodiversitet och störning lite grann, så spelar det även roll hur stark konkurrensen mellan arter och nyetableringen av arter är, samt vilket mått på biologisk mångfald som används i studien.

LIST OF PAPERS

This thesis is a summary of the following papers:

- Paper **I** Svensson, J. R., M. Lindegarth, M. Siccha, M. Lenz, M. Molis, M. Wahl, and H. Pavia. 2007. Maximum species richness at intermediate frequencies of disturbance: Consistency among levels of productivity. *Ecology* **88**:830-838.
- Paper **II** Svensson, J. R., M. Lindegarth, and H. Pavia. 2009. Equal rates of disturbance cause different patterns of diversity. *Ecology* **90**:496-505.
- Paper **III** Svensson, J. R., M. Lindegarth, and H. Pavia. 2010b. Physical and biological disturbances interact differently with productivity: effects on floral and faunal richness. *Ecology* **91**:3069-3080.
- Paper **IV** Svensson, J. R., M. Lindegarth, P. R. Jonsson, and H. Pavia. The Intermediate Disturbance Hypothesis predicts different effects on species richness and evenness. Manuscript.

Papers **I**, **II** and **III** was reprinted with the kind permission of from the Ecological Society of America.

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What is ecological disturbance, really?

Since this thesis is entirely devoted to ecological disturbances, we might as well start at the beginning. That is, to elucidate the concept of 'disturbance'. There are quite a few definitions of disturbance that I will explain and discuss in the first section, whereafter I move on to agents of disturbance, followed by measures and components of disturbance. An agent of disturbance is the instrument that causes the damage, such as an animal, waves or fire. The components of disturbance are the properties of the damaging force of the disturbance agent, i.e. the heat of the fire, the strength of the waves and the extent of borrowing by an animal. The issues regarding agents and components of disturbance are discussed in paper **I** and specifically tested in papers **II** and **III**. Should I not have failed entirely in my attempt at illuminating the audience on the topic of disturbance in these earlier sections, she or he will have an appropriate background for the following sections on ecological theories on disturbance. More specifically, I will sort out the most prominent hypotheses and models on the effects of disturbance on biodiversity, i.e. the Intermediate Disturbance Hypothesis (IDH) and the Dynamic Equilibrium Model (DEM), as well as a few related models on colonization and the specific components of disturbance. The IDH predicts maximum diversity at intermediate levels of disturbance, whereas the DEM predicts that the level of disturbance required to maximize diversity depends on the level of productivity. The IDH is tested by manipulative experimentation in papers **I-III** and theoretically evaluated in paper **IV**, and tests of the DEM is incorporated in the experiments in papers **I** and **III**. Furthermore, I will present and discuss a number of possible prerequisites, or assumptions, which these models may rely on. In conclusion, readers that have the stamina to go through the entire thesis will be handsomely rewarded by superior knowledge about definitions, agents and components of disturbance as well as of theories on disturbance and their associated predicaments. Hence, they will know what ecological disturbance really is.

Definitions of disturbance

There are quite a few definitions of disturbance, which may or may not help the reader depending on their complexity and explicitness. The most straightforward definition is that by Grime (1977), who defines disturbance as partial or total destruction of biomass. Although simplicity is something to strive for, especially to increase the operationalization of a definition for manipulative experiments, a too simple definition can include processes and mechanism that may in fact only have a marginal effect on species assemblages. The definition by Pickett and White (1985) where disturbance is "...any relative discrete event in time that disrupts ecosystems, community, or population structure and changes resources, substrate availability, or the physical environment", is also very broad. Although this definition is undoubtedly more explicit, it still encompasses many events that occur naturally and frequently without necessarily have any measurable effects on either diversity or density of species. An extension to this definition was added by Pickett et al. (1989), in which "Disturbance is a change in the minimal structure caused by a factor external to the level of interest". A benefit with this hierarchical view of disturbance is that one must consider the scale at which a certain disturbance operates. For instance, an herbivorous insect can be a disturbance to the leaves of a single tree, whereas if the study site is an entire forest it may be more relevant to consider wind-throws by hurricanes or large scale forest fires. However, this hierarchal view does not compensate for the drawbacks of the broadness of the original definition.

Notable distinctions in definitions comes from of Pain and Levin (1981) and Reynolds et al. (1993), who argue that disturbance should be defined exclusively based on its measurable

effect on ecological communities. In contrast to descriptions encompassing a range of different processes (c.f. Pickett and White 1985). According to Pain and Levin (1981), “Patch birth rate, and mean and maximum size at birth” can be used as “adequate indices of disturbance.” The definition of a ‘patch’ here is the primary substratum, i.e. space, that is affected by the disturbance. Similarly, Reynolds et al. (1993) defines disturbances as “primarily non-biotic, stochastic events that results in distinct and abrupt changes in the composition and which interfere with internally-driven progress towards self-organisation and ecological equilibrium; such events are understood to operate through the medium of (e.g.) weather and at the frequency scale of algal generation times”. As indicated by the subordinate clause in this definition, it is explicitly intended for studies on phytoplankton, and the definition by Pain and Levin (1981) only holds for communities where primary space is the limiting resource. Hence, while both definitions are useful within their own fields of study, they will not hold for ecological studies on disturbance and diversity in general.

The more operational definitions of disturbance include the alterations of resources as a consequence of a disturbing force. For instance, Shea et al. (2004) define disturbance as an event which “alters the niche opportunities available to the species in a system” by removing biomass and “freeing up resources for other organisms to use” or in any other way cause “a direct shift in available nutrients”. Similarly, Mackey and Currie (2000) define disturbance as “a force often abrupt and unpredictable, with a duration shorter than the time between disturbance events, that kills or badly damages organisms and alters the availability of resources”. The inclusion of freeing of resources is important because this is the characteristic of a disturbance which may ultimately lead to a positive effect on diversity, if the availability of resources enables, or maintains, coexistence in a community. According to Sousa (1984), disturbance is defined as “...a discrete, punctuated killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.” Hence, instead of considering availability or resources, which may or may not affect recruitment, this definition goes straight to the core of the potential for a disturbance to mediate coexistence. That is, opportunities for recruitment created, directly or indirectly, by disturbance, because without new species recruiting into the space freed by disturbance diversity cannot increase (Osman 1977, Collins et al. 1995, Huxham et al. 2000). Thus, like many other researchers, I find this definition of disturbance to be the most practical and operational for investigations of patterns between diversity and disturbance. Consequently, the definition of disturbance by Sousa (1984) will be used throughout this thesis, with the addition that the disturbance should be ecologically relevant for the system under study. Similar to the arguments by Pickett et al. (1989), a disturbance should be considered in relation to scale, but also to relevance of agents and components of disturbance for the specific system and/or the phenomena the model or hypothesis is intended to explain.

Agents of disturbance

The mechanisms and processes that are inflicting damage upon species assemblages are called agents of disturbance. Commonly, researchers on disturbance distinguish between biological and physical agents of disturbance (McGuinness 1987, Wootton 1998, Sousa 2001), while some authors use more explicit subdivision (Menge and Sutherland 1987). In order to give a clear picture of what these agents are, I will describe some of the more common agents of disturbance used in previous studies. Examples of agents of physical disturbance include anoxia (Diaz and Rosenberg 1995), boat traffic (Willby et al. 2001), desiccation (Lenz et al. 2004), deposition (Miyake and Nakano 2002), drifting logs (Dayton 1971), erosion (Fox

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1981), fire (Eggeling 1947), floods (Lake et al. 1989), ice-scouring (Gutt and Piepenburg 2003), pesticides (Szentkiralyi and Kozar 1991), pollution (Benedetti-Cecchi et al. 2001), sediment movement (Cowie et al. 2000), temperature (Flöder and Sommer 1999), tilling (Wilson and Tilman 2002), trawling (Tuck et al. 1998), tree poisoning (Sheil 2001), tree lopping (Vetaas 1997), wind (Molino and Sabatier 2001), wave action (McGuinness 1987), and even warfare (Rapport et al. 1985). Biological disturbances are mainly predation (Talbot et al. 1978) and grazing (Collins 1987), although some authors add algal whiplash (Dayton 1975), burrowing (Guo 1996), disease (Ayling 1981), parasites (Mouritsen and Poulin 2005) and trampling (Eggeling 1947).



Fig. 1 Disturbance treatment in papers I and II. Physical scraping of settling panels removing all organisms from a given percentage (i.e. 20 or 40 %) of the panel at each disturbance event.

Due to the differences among these agents of disturbance, agents are commonly divided into groups based on their functional or mechanical characterizations. Menge and Sutherland (1987) divide the agents of disturbance into four different groups: physical disturbance, physiological disturbance, biological disturbance and predation/grazing. Physical disturbance is produced by mechanical forces (e.g. movement of air, water, and sediment), whereas physiological disturbance is the lethal effects produced by biochemical reactions (influenced by e.g. temperature, light or salinity). Biological disturbance is the lethal effects of the activities of mobile animals (e.g. trampling, burrowing, and digging), and predation and grazing is defined as mortality resulting from consumption by animals. In a similar fashion, Wootton (1998) suggests that the effects of consumers should be considered separate to the effects from physical disturbance, because “the biota of the community is less likely to directly control the dynamics of the latter”. That is, agents of biological disturbance may be density dependent to a much higher degree than agents of physical disturbance.

An even more important distinction between agents, than those given above, is based on their possibility for selectiveness in the damage they exert. Grazing and predation have been argued to be unsuitable agents of disturbance in studies on disturbance-diversity patterns, because consumers, unlike physical agents, may have preferences in prey species (e.g. McGuinness 1987, Sousa 2001). Due to this predicament, Sousa (2001)

reserves the term disturbance to include “damage, displacement or mortality caused by physical agents or incidentally by biotic agents”, thus, excluding consumption by grazers and predators. Since this possible high degree of selectivity has no comparison in physical disturbances, outcomes of studies on disturbance using biological agents may be confounded and, therefore, not generally applicable. For instance, if a consumer prefers prey species that are inferior competitors, this biological disturbance will increase the rate of competitive exclusion instead of breaking the dominance of competitive superiors. This degree of selectivity may be even more complex in disturbance-diversity models that include productivity, i.e. the DEM, because grazers have been shown to prefer plants with higher nutrient content in both terrestrial (Onuf et al. 1977) and marine systems (Cruz-Rivera and Hay 2000). Accordingly, in paper **III** I show that a biological disturbance (grazing by periwinkles) and productivity interactively affected the number of macroalgal species, whereas the physical disturbance (wave-action) only affected the number of invertebrate species in natural marine epilithic assemblages. These patterns were, in part, explained by differences in the degree of selectivity between disturbances. Accordingly, the non-selective physical disturbance (scraping) in papers **I** and **II** (Fig. 1) affected all groups of species in the hard-substratum assemblages; annelids, barnacles, bryozoans, hydroids, mussels, sea-anemones, sponges and tunicates, as well as green, brown and red macroalgae. Thus, in contrast to the plain distinction between biological and physical agents of disturbance, a more operationally beneficial distinction may be that between selective and non-selective agents of disturbance.

Components and quantities of disturbance

In relation to agents of disturbance, i.e. ‘what is disturbing’, there are also components of disturbance, i.e. ‘how is it disturbing’. These components, also called attributes (Shea et al. 2004), commonly differ in the way they are characterized and measured. According to Osman and Whitlatch (1978), “a disturbance agent will have two components, frequency and magnitude”, where frequency is how often a patch is disturbed and the magnitude refers to the number of disturbed patches. Wootton (1998) identifies three components of disturbance “increasing average mortality, increasing temporal variability, and increasing spatial heterogeneity”. There are, however, many more components of disturbance. These may be divided into conceptual and operational terms of disturbance. The conceptual terms; level, intensity, severity, magnitude, regime, timing, and shape, are intended to verbally explain or describe aspects of disturbance, whereas the operational; frequency, extent, duration, time, size, rate and predictability, can be measured using their defined quantities (Table 1).

The drawback with the inexplicitly defined conceptual terms is that they are not easily generalized among studies. For example, ‘intensity’ has been used to describe a variety of experimental manipulations and variables, such as penetration depth per bite by limpets (Steneck et al. 1991), type of mechanical scrubbing (McCabe and Gotelli 2000) and degree of oscillation in sediment (Garstecki and Wickham 2003). Similarly, ‘magnitude’ can be a general description, occasionally used synonymously to level, intensity and severity. However, magnitude can also be used for more specific measures, such as the number of patches affected by disturbance (Osman and Whitlatch 1978) and the percentage of biomass removed by floods (Kimmerer and Allen 1982). The fact that the units and meaning of disturbance can be unclear, and differ among studies (Pickett and White 1985, Sousa 2001, Shea et al. 2004), may be a consequence of the unclear formulations of the hypotheses the studies aim to test. This is because the most prominent models on patterns between disturbance and diversity (see section: ecological theories on disturbance) are conceptual

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models based on relatively scaled variables (Schoener 1972, Peters 1991). However, in order to evaluate general ecological theories, it is important that concepts are commensurable among studies.

Table 1 Conceptual and operational terms of disturbance commonly used in ecological studies.

Term	Meaning	Quantity
<i><u>Conceptual</u></i>		
'regime'	Generic term for the types and components of disturbance currently acting in a given area	-
'level'	General description of overall amount of disturbance	-
'severity'	General description used synonymously to intensity and magnitude, and/or specific for damage caused	-
'intensity'	General description used synonymously to severity and magnitude, and/or specific for disturbing force	-
'magnitude'	General description, but also used synonymously to severity and intensity	-
'timing'	When a disturbance occurs and influence of the current conditions at that time	-
'shape'	Specific shape (i.e. oval, rectangular, square) of two- or three-dimensional space disturbed	-
<i><u>Operational</u></i>		
'frequency'	Number of disturbance events per unit time	time^{-1}
'time'	Period of time since last disturbance event	time
'duration'	The amount of time a disturbance event lasts	time
'phasing'	Temporal pattern of disturbance	"S", i.e. time
'predictability'	Variance in mean time between disturbances	variance
'size'	Size of an individual disturbance events	area
'extent'	Total two- or three-dimensional space disturbed	area or volume
'rate'	Product of area and frequency	$\text{area} \times \text{time}^{-1}$

One effort to increase the commensurability among studies on disturbance is the proposal of the term 'rate' of disturbance by Miller (1982), where rate is the sum of the size of all disturbance events in a given area per unit time, i.e. the product of area and frequency of disturbance. This is comparable to the argument of Osman and Whitlach (1978), who suggested that disturbance is composed of the two components frequency and magnitude, although they did not suggest a general joint measure. Similarly, Petraitis et al. (1989) defines 'intensity' as the product of area and frequency (not be confused with the common definition of the term intensity; Connell 1978, Sousa 1984, Shea et al. 2004). Taking into account the combined effects of area and frequency is important, because information about one of these components makes little sense without the context of the other. For instance, specifying an experimental manipulation where a community is disturbed once a week is completely

uninformative if we do not know the extent of the damage. Without doubt, the differences in effects on diversity will differ massively if the area disturbed each week is 1% of the total area compared to if it is 99%. However, disturbances composed of area and frequency are not the only ones that would benefit from a measure that combines the quantities of components. For example, in experiments on forest fires the temperature is vital for the effects on communities (e.g. Gignoux et al. 1997), and this can be combined with both the extent and the duration for increased commensurability among studies. Although the combined effects of disturbance components are always implicit in experimental studies, it is necessary to transform the measure of disturbance into a joint measure, i.e. rate, in order to put any experimental result into a wider context, and to allow for direct and meaningful comparisons among studies.

The main benefit of careful specifications of the components of disturbance is that they give information of the manner in which a particular disturbance is exerted. Even for joint measures, such as rate, it is important to specify each component clearly. This is important because disturbances that are equal in extent can nonetheless have significantly different effects on diversity, depending on how the disturbance is distributed (Bertocci et al. 2005, papers II and III). In paper II I show that equal rates of disturbance may still give different patterns in diversity depending on the specific combination of area and frequency, i.e. the regime of disturbance. In accordance with the predictions by Miller (1982), the regime with small, frequent disturbances favoured colonizing species, whereas large, less frequent disturbances favoured competitive dominants. On a similar note, Bender et al. (1984) identified two different types of disturbance, pulse and press, defined as instantaneous alteration of species number (pulse) and the sustained alteration of species densities (press). The distinction between two clearly different mechanisms of disturbance, which may nonetheless be equal in total extent, can be useful for predictions of patterns of diversity. In paper III, the biological, continuous small-scale, disturbance (i.e. press) differed in effects on diversity from the physical disturbance, instantaneous removal or damage of individuals (i.e. pulse). This shows that clear specification of components of disturbance is important, because the way the damage of a given disturbance is exerted can be vital for the outcome of studies on disturbance-diversity patterns.

Differences between Disturbance, Perturbation and Stress

In ecological studies, the two concepts 'perturbation' and 'stress' are often used synonymously to disturbance (e.g. Connell 1978, Bender et al. 1984, Rapport et al. 1985). Processes and mechanisms that are generally described as disturbance may instead be classified as either perturbation (Webster and Patten 1979, Lane 1986) or stress (e.g. McGuinness 1987), and the terms perturbation and stress are often used interchangeably with disturbance without explicitly definitions of any of the terms (e.g. Caswell and Real 1987, Davies et al. 1999). Similarly, the term perturbation can be used to refer to the effects of stress on a system (Petraitis et al. 1989) and the term stress can be used to describe a perturbation (Odum et al. 1979). That these three terms are used haphazardly can be problematic, because definitions of ecological phenomena may be vital for experimental design in tests of hypotheses. Especially, since the concept of disturbance is in itself a quagmire, confounding it with stress or perturbation would be severely suboptimal.

The most clear distinction among these three terms is that between disturbance and stress, where disturbance is generally considered to cause more severe damage (Grime 1977, Pickett et al. 1989, Wootton 1998). Among the most common mechanisms and processes

described as stress are desiccation (Dayton 1971), pollutant discharges (Rapport et al. 1985) and fluctuations in temperature (Jackson 1977), nutrients (Menge and Sutherland 1987) and light (Grime 1977). According to Grime (1977) stress in plant communities is defined as “the external constraints which limit the rate of dry-matter production of all or part of the vegetation”, which is clearly distinct from disturbance events that “limit the plant biomass by causing its destruction”. Wootton (1998) makes a similar distinction between stress and disturbance, where the upper limit of what can be defined as stress is mortality. Stress is here defined by “causing changes in performance as opposed to mortality”, and he states that stress can also “reduce conversion efficiency or increase metabolic costs”. This view is also shared by Sousa (2001) who states that the difference between disturbance and stress, although possibly caused by the same agent, is that disturbance only occurs when “an organisms tolerance is exceeded, resulting in its death or sufficient loss of biomass that the recruitment or survival of other individuals is affected”. Pickett et al. (1989) defines stress as a “change in the interaction maintaining a minimal structure”, caused “directly or indirectly by an external factor”. For example, an herbivorous insect can be a disturbance to a leaf by disrupting its physiological integrity, but a stress to the plant because leaf damage may affect the performance and reproduction of the plant. Thus, the same mechanism will be classified as either disturbance or stress depending on the level of interest (Pickett et al. 1989). Rapport et al. (1985) defines stress as “an external force or factor, or stimulus that causes changes in the ecosystem, or causes the ecosystem to respond, or entrains ecosystemic dysfunctions that may exhibit symptoms”. This definition is not among the more operational, since it is only applicable at the ecosystem level and it is not intuitive what a symptom of an ecosystemic dysfunction may be. Another thought-provoking definition of stress is that by Rykiel in which stress is “a physiological or functional effect; the physiological response of an individual, or the functional response of a system caused by disturbance or other ecological process; relative to a specified reference condition; characterized by direction, magnitude, and persistence; a type of perturbation”. Thus, according to this definition, stress is a type of perturbation that is the effect of disturbance. Here, I much prefer the views of Grime (1977), Wootton (1998) and Sousa (2001), where stress is generally distinguished from disturbance as non-lethal effects and responses.

Agents of perturbation are commonly similar to those of disturbance and stress, such as flood scouring (Webster and Patten 1979), environmental variation (Lane 1986), alteration of species densities (Bender et al. 1984). Furthermore, this concept is also used for processes and mechanisms that are not easily defined, such as departure from a normal state (Pickett and White 1985), divergence in spatial organization of badger populations due to bovine tuberculosis (Tuytens et al. 2000) and the falling of leaves on spider webs (Leclerc 1991). Moreover, the term unperturbed is used by Padisak (1993) to describe systems unaffected by either disturbance or stress. Although definitions of perturbation are scarce in the literature, there are a few notable exceptions. Rykiel (1985) defines perturbation as “the response of an ecological component or system to disturbance or other ecological process as indicated by deviations in the values describing the properties of the component or system; relative to a specified reference condition; characterized by direction, magnitude, and persistence”. Hence, according to Rykiel (1985) disturbance is the agent causing damage whereas perturbation, as well as stress, is the effects of a disturbance. Distinguishing between the cause and effect of disturbances is not unimportant, for instance, if a process defined as disturbance does not invoke any measurable response in the recipient community it is questionable whether a disturbance has really occurred. However, this interpretation of the terms has not been widely accepted, which is likely due to the rather counter-intuitive terminology of stress- and

perturbation-causing disturbances. Another exception is the definition by Picket and White (1985), where perturbation is “a departure (explicitly defined) from a normal state, behaviour, or trajectory (also explicitly defined)”. Although this definition is rather unclear and exceptionally broad, it may in this case be both appropriate and useful. In the sense that Padiak (1993) uses the term, but in contrast to Rykiel (1985), it may be beneficial to reserve a word that describes process and mechanisms that can be either disturbance or stress, or in fact neither.

Ecological Theories on Disturbance

Disturbance has been recognized as a structuring force in ecological communities since the beginning of the last century (Cooper 1913). However, it was not until the 1970ies that disturbance was regarded as a key process in general ecological theory (Dayton 1971, Grime 1973, Levin and Paine 1974). Since then, a number of hypotheses have been proposed to address the involvement of disturbance in ecological phenomena. These hypotheses mainly concern succession and biodiversity (Connell 1978, Miller 1982, Dial and Roughgarden 1998), but also on evolutionary processes (Benmayor et al. 2008), biological invasions (Davis et al. 2000) and ecosystem functions (Cardinale and Palmer 2002). More recently, the productivity in natural communities, another key process in ecology (Connell and Orias 1964, Tilman 1980, Abrams 1995), has been suggested to act in concert with disturbance, which may explain more complex patterns in species diversity (Huston 1979, Kondoh 2001, Worm et al. 2002). The following sections will focus on the most common hypotheses and models on effects of disturbance on biological diversity, the interactive effects of disturbance and productivity, as well as possible assumptions or prerequisites that these models may rely on.

The Intermediate Disturbance Hypothesis (IDH)

The most prominent theory on disturbance, and possibly ecology in general, is the Intermediate Disturbance Hypothesis (IDH; Connell 1978) (Fig. 2). The original paper by Connell (1978) has been cited over 3300 times and the IDH also represents one of few well established ecological theories with an impact on management of marine and terrestrial national reserves and parks, e.g. Yellowstone National Park, USA (Wootton 1998). The origin of the IDH is, however, debated (Wilkinson 1999). Even though J. H. Connell is commonly credited as the originator of the IDH, his main argumentation relies on the much earlier work of Eggeling (1947) on patterns of diversity in African rain forests (see: Fig. 1 in Connell 1978). In his article, Wilkinson (1999) also identifies three well-known authors who all, prior to the work of Connell, discussed relatively higher diversity at some form of intermediate level of disturbance; E. P. Odum (1963), J. P. Grime (1973), and H. S. Horn (1975). Similarly, Osman (1977) identified “an optimal frequency of disturbance at which diversity is maximized” in his study on marine epifaunal communities, which he argues is caused by reductions at high and low levels of disturbance “because of a decrease in the number of species present or an increase in dominance”. Surprisingly, neither of Odum (1963), Grime (1973), Horn (1975) or Osman (1977) is cited in the review article by Connell (1978).

The IDH predicts that diversity will reach its maximum at intermediate levels of disturbance, while remaining low at high and low levels of disturbance (Fig. 2). The rationale for this is that at low levels of disturbance strong competitors exclude competitively inferior species and communities are dominated by a few species. Intermediate levels of disturbance, however, disrupt competitive hierarchies by increasing levels of mortality and thus making free space

available for recruitment of competitively inferior species. At successively higher levels of disturbance, recruitment cannot balance the high levels of mortality and slow recruiting

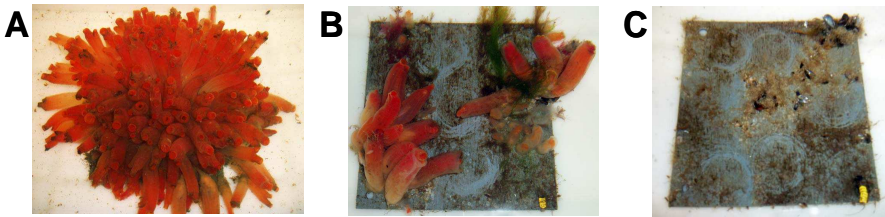
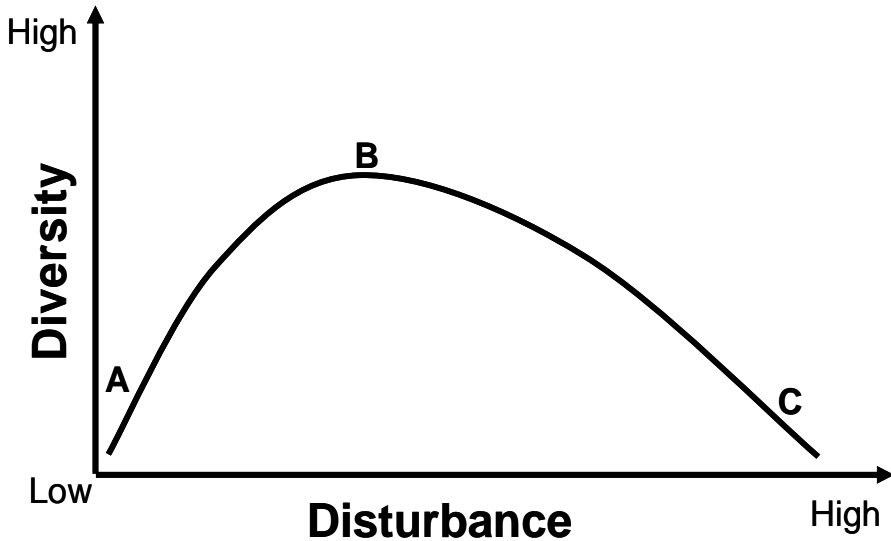


Fig. 2 The hump-shaped pattern between disturbance and diversity as predicted by the Intermediate Disturbance Hypothesis (IDH). The mechanisms of the IDH are illustrated by settling panels (A, B and C) used in papers **I** and **II**. At point A diversity is low due to competitive exclusion, at point B coexistence is enabled by freeing space for new species, and at point C few species survive due to high level of disturbance.

species disappear from the community. The drawback of this straightforward logic, and hence its conceptual appeal, is that it has received criticism from both empirical and theoretical studies for being too simplistic (Pacala and Rees 1998, Huxham et al. 2000, Shea et al. 2004). Furthermore, a literature review revealed that only 20 % of the studies on effects of disturbance on diversity showed the unimodal pattern predicted by the IDH (Mackey and Currie 2001). Nevertheless, the IDH has been supported in field experiments in terrestrial (e.g. Armesto and Pickett 1985, Collins 1987, Molino and Sabatier 2001), freshwater (e.g. Padisak 1993, Reynolds 1995, Flöder and Sommer 1999) and marine communities (e.g. Osman 1977, Sousa 1979a, Valdivia et al. 2005), as well as in laboratory experiments (e.g. Widdicombe and Austen 1999, Buckling et al. 2000, Cowie et al. 2000) and model evaluations (Petraitis et al. 1989, Dial and Roughgarden 1998, Li et al. 2004). In accordance with these studies, the characteristic hump-shape pattern between disturbance and diversity was observed in papers **I**, **II** and **IV**.

The apparent simplicity of the IDH may, however, be slightly deceiving. There are, in fact, many aspects of the IDH and the way that disturbance may determine levels of diversity. Although I will spare the reader yet another section on components of disturbance, there are

some fundamental differences among the mechanisms of disturbance in relation to the hypothesis that should be noted. For instance, how often a disturbance occurs (i.e. frequency), how large the disturbance is (i.e. area or extent) and time since the last disturbance (i.e. time). Even though they are all interrelated, through the main rationale of disrupting competitive exclusion, the underlying mechanisms may be different. In the case of frequency, high levels of diversity can be maintained if the disturbance events occur often enough to prevent any one species from achieving dominance, while not occurring so often that only few species can persist. When the extent of disturbance is considered, areas that are too large will eliminate all species, areas that are too small will have little or no impact, whereas intermediate areas may disrupt competitive exclusion and allow establishment of new species in the disturbed patches. In comparison, the time aspect states that high diversity will be observed at some point in time after recolonization of the disturbed area, but before the community returns to its successional climax (i.e. dominance by few species). The main difference here is commonly referred to as the 'between patch' vs. 'within patch' mechanisms (e.g. Wilson 1990), or sometimes as the resetting of a patch successional clock vs. the creation of a successional mosaic (e.g. Chesson and Huntly 1997). This distinction is articulated in a straightforward way by Wilson (1994): "A single patch does not have a frequency of disturbance, only a time since last disturbance". Albeit a bit drastic, it has been suggested that the within patch aspect is not a mechanisms of coexistence, as much as a mere observation of succession (Wilson 1990, Wilson 1994, Chesson and Huntly 1997). In contrast, the successional mosaic, or between patch, explanation relies on disturbances occurring in a greater area, where disturbed patches are all in different stages of succession and may, thus, together compose a high regional diversity (Levin and Paine 1974, Chesson and Huntly 1997, Sheil and Burslem 2003).

One way to resolve the discussion about the differences between the within-patch and the between-patch mechanisms of the IDH, could be to consider the different components of disturbance, i.e. how the damage from the disturbance is exerted. Bender et al. (1984) distinguishes between 'pulse disturbance', i.e. instantaneous alteration of species number, and 'press disturbance', i.e. the sustained alteration of species densities (see also section 'Components and quantities of disturbance'). A press disturbance could unceasingly prevent competitive exclusion of a dominant species, which yields higher within-patch diversity. In contrast, a pulse disturbance would provide patches of different successional stages and ages (younger more r-selected and older more K-selected species), giving rise to the higher between-patch diversity. Hence, this subdivision of disturbance could perhaps be a missing link in the so far unresolved issue (see Sheil and Burslem 2003) of differentiating the within-patch from the between-patch mechanisms of the IDH.

The Dynamic Equilibrium Model (DEM)

The Dynamic Equilibrium Model (DEM; Huston 1979, Kondoh 2001) relies on the same general coexistence mechanisms as the IDH (Fig. 3). At low levels of disturbance one, or few, species will dominate and exclude all other species, and at high levels of disturbance very few species can persist, while coexistence is possible at intermediate levels. The addition in the multifactorial model DEM is that the relationship between disturbance and diversity is modified by the level of productivity. Huston (1979) suggested that increased productivity, and thus growth rates of individuals and populations, means that a more severe disturbance is required to prevent competitive exclusion. Consequently, at low productivity, and slow growth rates, maximum diversity is observed already at low levels of disturbance because competitive exclusion occurs at a lower rate. Thus, the shape of the relationship between

disturbance and diversity is predicted to be of three general types: monotonically decreasing (at low productivity), unimodal (when productivity is intermediate) and monotonically increasing (when productivity is high). Although the DEM has not been experimentally evaluated nearly as much as the IDH, there are corroborating manipulative studies from aquatic as well as terrestrial systems (e.g. Turkington et al. 1993, Worm et al. 2002, Jara et al. 2006). However, in paper I, there was no effect on diversity of the manipulated increase in productivity, whereas maximum species richness was observed at intermediate levels of physical disturbance, in accordance with the IDH. This is likely explained by the productivity treatment, which, despite a general effect on growth rates of algae, did not affect the competitive dominants in the hard substratum assemblages. Thus, the rate of competitive exclusion was not measurably affected and more frequent disturbance was consequently not required to prevent exclusion of inferior competitors at high levels of productivity.

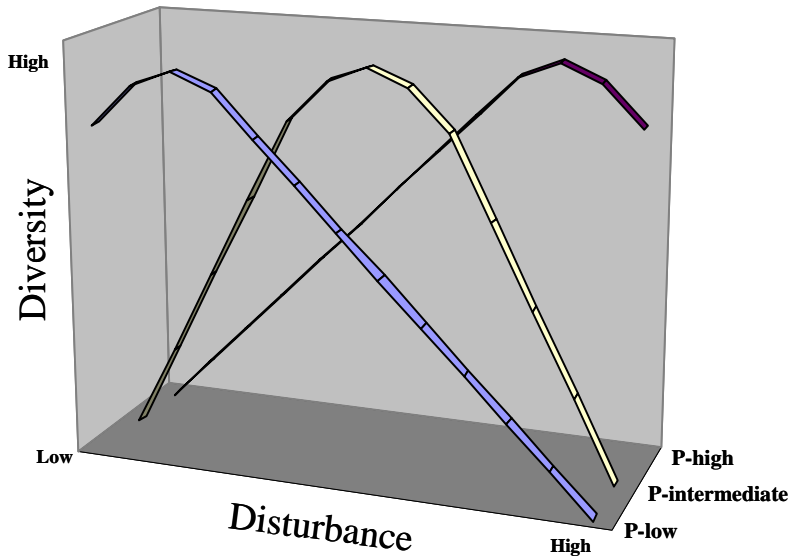


Fig. 3 The patterns predicted by the Dynamic Equilibrium Model (DEM). At low levels of productivity, maximum diversity is observed already at low levels of disturbance due to low rates of competitive exclusion. At intermediate levels of productivity intermediate levels of disturbance is required, and high levels of productivity high levels of disturbance is required, in order to disrupt competitive exclusion by dominants and free resources for colonizing species.

Similar to the IDH, agents and components of disturbance may influence the outcome of tests on the DEM. For instance, biological and physical agents may differ in selectivity (McGuinness 1987, Wootton 1998, Sousa 2001) and consumers often prefer prey with higher nutrient content (Emlen 1966, Onuf et al. 1977, Pavia and Brock 2000). One indication of a discrepancy between agents of disturbance is that interactive effects between biological disturbance and productivity has been observed in many studies from various environments (see Proulx and Mazumder 1998 and references therein), whereas tests of the DEM using physical disturbance have more variable outcomes (e.g. Turkington et al. 1993, Death and Winterbourn 1995, Death 2002, Jara et al. 2006). In paper III, in order to test for possible differences among agents, I contrasted the effects of a biological to that of a physical disturbance in an experiment on the DEM. Using natural sessile assemblages on boulders (i.e. epilithic communities) composed of invertebrates and macroalgae, I tested for interactive

effects between productivity (high vs. ambient), physical disturbance (simulated wave-action at five distinct frequencies) and biological disturbance (grazing by periwinkles manipulated as absent or present). The number of algal species was interactively affected by productivity and biological disturbance, whereas the invertebrate richness was affected by physical disturbance only. This may in part be explained by difference in degree of selectivity between agents, but, more interestingly, also in the way the damage is exerted. When biomass is slowly reduced, as exerted by the biological, continuous small-scale disturbance (i.e. press disturbance; Bender et al. 1984), this effect can more easily be counteracted by increased growth of the affected organisms (Huston 1979, Kondoh 2001). In contrast, increased individual growth rate cannot easily compensate for instantaneous loss of individuals, as exerted by the physical disturbance (i.e. pulse disturbance; Bender et al. 1984). In accordance with these arguments and our results, Kneitel and Chase (2004), the only previous study that has tested for interactions of all three factors, also found that biological disturbance (predation), but not physical disturbance (drying), and productivity interactively affected species richness. Thus, agents and components of disturbance may not only influence disturbance-diversity patterns, but also the specific interactive effects between disturbance and productivity on biological diversity of natural communities.

Additional related models

The only model on effects of disturbance on diversity that specifically considers the different components of disturbance is that by Miller (1982). In his article, he introduces the term 'rate' of disturbance, i.e. the product of area and frequency, which, thus, takes into account the total amount of disturbance inflicted upon a community (see also section 'Components and quantities of disturbance'). According to Miller (1982), small, frequent disturbances favour species with rapid vegetative growth (i.e. 'competitors'), whereas large, less frequent disturbances favour species with high capacity for dispersal (i.e. 'colonizers') due to the differences in perimeter to area ratios among patches. Although Miller (1982) predominantly focuses on the area of disturbance, the other component of the rate, frequency, is equally important. Similar to variations in area, differences in frequency and timing of disturbance will influence the abundance and composition of natural communities (Sousa 2002). This is because species are likely to increase in abundance when the disturbance regime matches their preferred recruitment time (Underwood and Anderson 1994, Crawley 2004). Furthermore, because of the natural large variation in temporal distribution of propagules among species (Roughgarden et al. 1988, Underwood and Anderson 1994) a single large disturbance can only be colonized by the propagules that are available at the specific time when a limiting resource, i.e. space, is made free. In paper **II** I tested the model by Miller (1982), or more specifically if the specific combination of area and frequency matters even if the rate is kept constant. In accordance with the predictions by Miller (1982), the regime with small, frequent disturbances favoured colonizing species, whereas large, less frequent disturbances favoured competitive dominants. Thus, as is claimed in the title, equal rates of disturbance did cause different patterns in diversity.

In a model on the importance of the timing of disturbance, Abugov (1982) introduces the concept of disturbance 'phasing'. Abugov (1982) distinguishes between disturbances that are phased compared to those that are unphased. A phased disturbance means that all patches are cleared simultaneously, and the patches are termed to be 'in phase'. Conversely, during unphased disturbance, the probability of a patch being cleared by disturbance is independent of the disturbance of other patches. Phased disturbances are considered to be more large scale disturbance events such as storms or forest fires, whereas constant predation is given as an

example of unphased disturbance. The outcome of Abugov's model showed that highest diversity always occurred at intermediate levels of disturbance, regardless of the degree of phasing, but also that the diversity at any given level of disturbance depend on the degree of phasing. Furthermore, similar to the multifactorial model DEM, high levels of diversity was observed at intermediate degree of phasing at intermediate levels of disturbance. The idea of phasing is similar to that of temporal variability in disturbance, which has been shown to affect the community structure of benthic assemblages on rocky shores (i.e. Bertocci et al. 2005, but see: Sugden et al. 2007). It is also similar to the concepts of 'Nonadditivity' (Chesson 2000), 'Storage Effect' (Chesson and Huntly 1997) and 'Spatiotemporal Niche Creation' (Pacala and Rees 1998). The key argumentation in these concepts is that coexistence is enabled because different species utilize different spatiotemporal niches. The spatiotemporal niches may differ, depending on environmental fluctuations or disturbance, in the amount of available resources, the free space for settling and in their current stage of succession (Amarasekare et al. 2004, Roxburgh et al. 2004, Shea et al. 2004). Due to the suggestions of coexistence mechanisms that are consider to be alternative, the IDH and the DEM have been argued to give "inadequate, inconsistent, or improbable explanations" of species coexistence (see: Chesson and Huntly 1997). However, the main mechanism of coexistence in all these concepts, including phasing and temporal variability, is that different patches are at different successional stages and/or differ in availability of resources. Hence, it could be argued that they are all describing the 'between-patch', or 'successional mosaic', aspect of the IDH, where coexistence is maintained, or enabled, by disturbance, because patches at different stages in succession differ in species composition.

In their investigation of the theoretical validity of the IDH, Dial and Roughgarden (1998) found what they call 'the intermediate area hypothesis' and 'the intermediate recruitment hypothesis'. In contrast to most other models on disturbance (Petraitis et al. 1989, Chesson and Huntly 1997, Kondoh 2001), their mathematical model incorporates the dynamics of pelagic larvae and benthic adults, as well as hierarchal competition for the limiting resource space. The larval-benthic dynamics was purposely considered because the pattern predicted by the IDH is often observed in communities where species have long-lived propagules and space-limited adults, such as marine invertebrates, macroalgae and seed plants (Sousa 1979a, Sousa 1979b, Molino and Sabatier 2001, Jara et al. 2006). More specifically, in these systems the disturbance only affects the sessile adults, while leaving the propagule mortality unaffected (Dial and Roughgarden 1998). The two key points of the outcome of the model was that the IDH is a moderate to high settlement phenomenon, and that a subordinate species must have an adaptation allowing it to survive and/or colonize at levels of disturbance that are lethal to the dominant, if disturbance, area, or settlement is to allow coexistence. According to Dial and Roughgarden (1998), these two key points show that the IDH is not a universal phenomenon, which also leads to the additional outcome of the model, the intermediate area and recruitment hypotheses. If the level of disturbance, at an intermediate value, is kept constant, intermediate levels of recruitment lead to coexistence among species. This is explained by the exclusion of the subordinate species of a dominant superior at high recruitment, and at low recruitment the dominant cannot exist. However, in their model, area is equivalent to settlement, thus, yielding a similar intermediate area effect, where smaller habitats can favour subordinate species' coexistence with a dominant species. Although it could be argued that the proposed hypotheses are in fact already inherent functions of the IDH, since diversity cannot increase if no new species settle (Osman 1977, Huxham et al. 2000, papers II and III), it may still be noteworthy to point out that disturbance is not the only way exclusion can be prevented and coexistence maintained. Furthermore, it gives important

insights in the underlying mechanisms of coexistence for the IDH, as well as the possible prerequisites for observing the pattern predicted by the IDH discussed in the next section.

Prerequisites for the IDH and the DEM

In response to the inconsistencies in the outcome of manipulative tests of the IDH (reviewed by Mackey and Currie 2001), several authors have suggested that the predictions of the IDH relies on a number of prerequisites. The most common prerequisites, or assumption, are competitive exclusion (Fuentes and Jaksic 1988), large regional species pool (Osman 1977), multiple stages in succession (Collins and Glenn 1997), nonlinear resource use (Chesson and Huntly 1997), availability of spatiotemporal niches (Pacala and Rees 1998) and trade-offs between competition and tolerance (Petraitis et al. 1989) and between competition and colonisation (Dial and Roughgarden 1998). Furthermore, Menge and Sutherland (1987) argued that the effects of disturbance depends on the amount of environmental stress in the system. However, the constructive criticism in the suggestions of the prerequisites primarily concerns aspects of two key processes; competition and colonization.

Aspects of Colonization

According to Dial and Roughgarden (1998), the IDH is a "moderate-to-high settlement phenomenon", and Collins et al. (1995) pointed out that it is settlement by propagules that may allow for increases in diversity, not disturbance *per se*. That colonization is important in order for disturbance to have a positive effect on diversity is intuitive and logic. Diversity cannot increase if there are no available propagules to occupy the space, or any other limiting resource, which is freed by disturbance (Sousa 2001). Another suggested prerequisite, that is equally straightforward, but maybe less intuitive, is the importance of a large regional species pool (Osman 1977). This is because diversity cannot increase if the propagules that establish in the cleared space, are the same species that originally inhabit the assemblage. This was clearly shown in a manipulative experiment by Huxham et al. (2000), where the species pool in the intertidal macrofaunal communities was too small to allow for settlement of new species in the assemblages subjected to disturbance. Low rate of colonization is also something that may explain the lack of positive effects of disturbance on diversity in paper **III** and at one of three sites in paper **II**. In the experiment on the effects of physical and biological disturbance and productivity on natural epilithic assemblages (paper **III**), the recruitment of new species occurred at a rate that was not sufficient to counteract the negative effects of disturbance. Similarly, in paper **II**, the physical disturbance did not have a significant effect on the richness of the hard substratum assemblages at one site, where richness was generally low and new species did not settle in disturbed patches. In contrast to paper **III**, this experiment was setup in the waters of the Tjörnö archipelago, where the regional species pool and availability of propagules per definition was natural. However, it has previously been shown that local hydrodynamics in areas near this site may hamper the settling of invertebrate larvae (Berntsson et al. 2004, Jonsson et al. 2004), which also could explain the surprisingly low total cover in the controls assemblages at this site. Thus, local hydrodynamics may be of equal importance to the availability of propagules and the size of the regional species pool, for the outcome of manipulative experiments on the effects of disturbance on diversity.

Aspects of Competition

The other key process in the suggested prerequisites, competition, was mentioned already by Connell (1978), who considered competitive exclusion to be an assumption for the coexistence facilitating mechanism of disturbance. Similar to the arguments for colonization, disturbance cannot increase diversity if there is no exclusion process to interrupt by removing the dominant(s) and allow new species to establish in a community (Huston 1979, Sousa 1984, 2001). This is also linked to the suggested trade-off between competition and colonization. If the inferior species cannot out-compete the dominant at colonizing newly freed substrata, competitive exclusion may not be prevented and diversity will not increase in response to disturbance (Dial and Roughgarden 1998). Similarly, for the trade-off between competition and disturbance tolerance, the inferior species must be better adapted to cope with destructive events, either by physiological tolerance or other means such as fast growth and re-colonization (Petraitis et al. 1989). Thus, in order for a disturbance to facilitate coexistence, the dominant species must be comparatively more susceptible to the damage exerted. Furthermore, the dominant species must also be able to maintain their competitive advantage in the absence of disturbance (Connell 1978). The importance of competition for the outcome of experiments on disturbance is clearly shown in paper II, where the three different responses to disturbance at the three different sites clearly corresponded to the differences in species composition (fig. 4). Competitive exclusion was evident at the site where support for the IDH was found, as also observed in paper I, whereas increasing levels of disturbance only decreased diversity at the site lacking clear dominants in the undisturbed controls. Although assemblages at the third site also lacked dominants, there was no effect of disturbance because the initial diversity was so low that even the limited colonization in this area could counteract the effects of disturbance. Consequently, the same disturbance can give widely different patterns in diversity depending on the composition of species, and the level of competition, in communities.

In order to disrupt the competitive advantage of dominants, the destructive event of a disturbance must potentially affect all species in a similar manner, or, conversely, fall heavier on the competitive dominants. The problem with possible selectivity of agents has been discussed for manipulations of disturbance, but not for manipulations of productivity. This lack of considerations of selectivity in agents may severely confound tests of the DEM. The DEM predicts that competitive exclusion will increase with productivity, thus requiring a stronger disturbance to be disrupted, but if the inferior competitors are more strongly affected by the productivity treatment this could instead slow down the rate of exclusion. This would cause diversity to peak at lower, rather than the predicted higher, intensities of disturbance. The issue of the selectivity of agents of productivity was clearly shown in paper I, where the IDH was supported, but the DEM was not. The most likely explanation for this outcome is that the dominant species exerting competitive exclusion, the tunicate *Ciona intestinalis*, was unlikely to benefit from the manipulation of nutrient availability. Hence, even though the productivity treatment had a general, positive, effect on growth rates in the assemblages, the rate of competitive exclusion did not increase, and higher levels of disturbance was consequently not required to maximize diversity. Even in studies that recognize the issue of selectivity, there is a practical difficulty of designing a non-selective agent of productivity in manipulative experiments. Experimental manipulation of productivity in tests of the DEM is commonly done indirectly, i.e. by adding nutrients or organic matter (Turkington et al. 1993, Widdicombe and Austen 2001, Worm et al. 2002, Kneitel and Chase 2004, Jara et al. 2006, Canning-Clode et al. 2008, Sugden et al. 2008). In such manipulations it is necessary to test independently whether the actual experimental treatment (the adding of nutrients or organic matter) has an effect on productivity. Without evidence for an actual increase in productivity

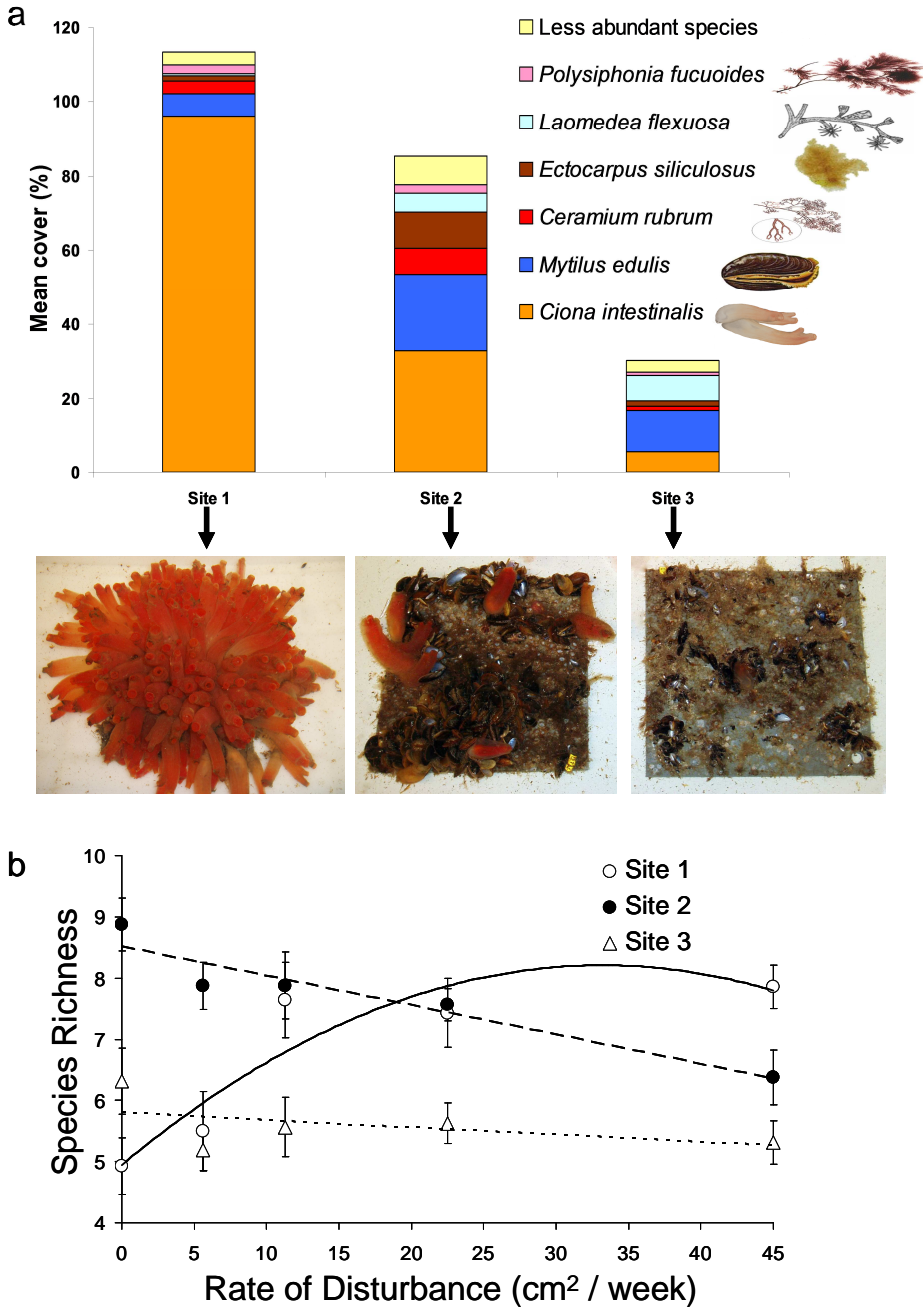


Fig 4 Three significantly different communities at sites 1, 2 and 3 which showed three different responses to disturbance in paper II. (a) Species composition, as well as pictures, of the control assemblages at sites 1, 2 and 3 and (b) responses to rates of physical disturbance, significant quadratic and linear quadratic components, respectively, at sites 1 and 2, and no significant pattern at site 3.

experiments cannot perform an adequate test of the DEM, and without information on the selectivity of the agent of productivity the outcome of tests cannot be adequately interpreted. Unfortunately, this issue is generally overlooked (e.g. Widdicombe and Austen 2001, Scholes et al. 2005, Jara et al. 2006). Nevertheless, if predictions about effects of productivity and disturbance on diversity are to be tested in field experiments, indirect manipulations, such as adding nutrients or organic matter, may be the only conceivable solution.

Considerations of diversity

Something that is conspicuously absent in the literature is a discussion on the potentially large variation in outcomes among studies depending on the measure of diversity that is used in tests of the IDH. As discussed in the earlier sections, nearly every aspect of disturbance has been considered, e.g. the definitions, the agents, the components, the quantities, how the damage from disturbance is exerted and a multitude of prerequisites have been suggested to explain inconsistencies in outcomes of the IDH. In addition, many other aspects of the IDH have been discussed, such as alternative mechanisms underlying coexistence (Pacala and Rees 1998), influence of the characteristics of communities (Fuentes and Jaksic 1988), interactive effects of disturbances (Collins 1987), importance of the specific traits of individual species (Haddad et al. 2008) and the context dependence of intermediacy (Shea et al. 2004). Yet, despite over 3300 citations of Connell (1978) and ample attention in the scientific literature, no one has considered the response variable for the conceptual model IDH, i.e. the aspect of diversity.

Consequently, in paper **IV** I investigated how the measure of diversity may affect the outcome of studies on effects of disturbance on diversity. This was done by scrutinizing the original formulations of the models, conducting a meta-analysis of previously published studies and through two different approaches to mathematical modelling. In the formulation of the IDH, Connell (1978) uses the word diversity without any further definition, while Huston (DEM; 1979) rejects all various indices and considers diversity to be solely richness and evenness. In the model presented by Miller (1982) diversity is defined as a measure that includes both “species abundance and number”. However, neither Huston nor Miller makes an effort to explain what kind of effects disturbance would have on species abundances in contrast to the number of species. In the meta-analysis I investigated if all measures of diversity show the same response in studies that use two or measures of diversity within the same experiment. The mathematical modelling was performed using one already established spatially implicit model (Kondoh 2001) and one spatially explicit automation model, in order to specifically contrast the responses to disturbance of the two major components of diversity: richness and evenness. Both models support the IDH when biodiversity is measured as species richness, but, in contrast, predict that evenness increases monotonically with increasing levels of disturbance. The meta-analysis showed that two-thirds of the published studies in the survey present different results for different diversity measures, and the comparisons between richness and evenness showed an even higher degree of dissimilarity. In addition, when the analyses from papers **I** and **II** were rerun to include evenness as response variable (these results were not included in any of the papers), the same patterns as in the models emerges. Hence, in accordance with the predictions of the two model, species richness was maximized at intermediate levels of disturbance, and evenness showed linear increases with increasing rates of disturbance (Evenness: linear component $MS=0.95$, $F=28.7$, $p<0.01$; $MS=1.75$, $F=81.8$, $p<0.01$, respectively, quadratic component $MS=0.010$, $F=0.30$, $p=0.58$; $MS=0.0052$, $F=0.24$, $p=0.63$, respectively, Fig. 5). Thus, the meta-analysis, as well as the

mathematical two models and the re-analysis of previous field experiments clearly show that the measure of diversity is vital for outcomes of tests of the IDH.

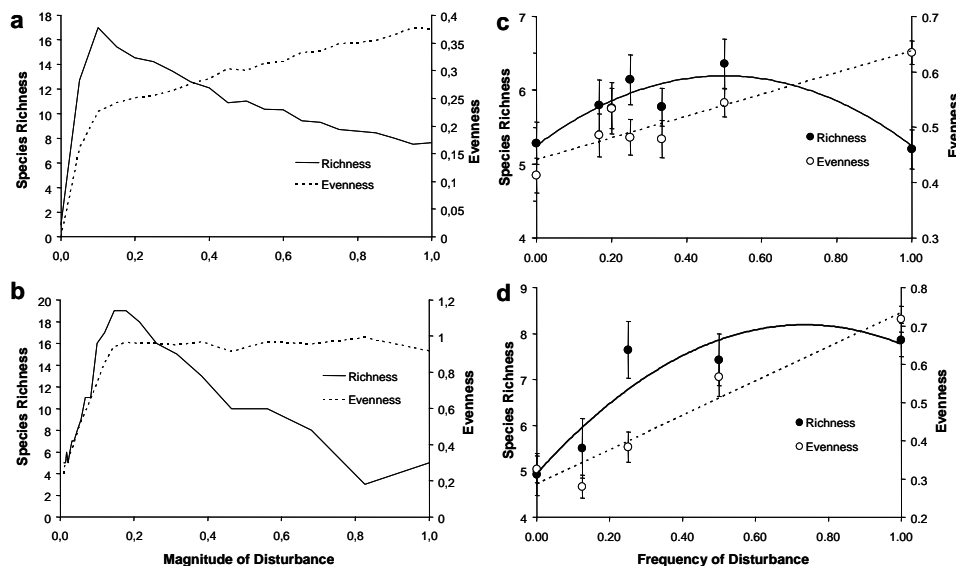


Fig. 5 Hump-shaped patterns between species richness and disturbance, but linear increases in evenness, in the two models from paper **IV** (a and b) as well as the re-analyzed results from the field experiments in papers **I** (c) and **II** (d).

Conclusions

In this thesis I have clearly (i.e. hopefully) shown that the definition of disturbance can influence the outcome of studies, depending on which characteristics of disturbances a particular definition encompasses. The type of agent that is causing the disturbance is crucial, because selectivity can differ among disturbance agents and biological agents may choose prey depending on nutritional value. Different components of disturbance can affect communities in different ways, and even the specific proportions of area and frequency within the same rate of disturbance can cause different patterns in diversity. The effects of disturbance will also to a large extent depend on the species composition of the community upon which it is inflicted. In tests of hypotheses on disturbance-diversity pattern, outcomes are generally influenced by the rate of competition, the availability of propagules, the regional species pool and interactions with the abiotic environment. Experimental tests of models that include productivity should also include explicit investigations of whether the manipulative treatment significantly affects the overall productivity, as well as the recognition of the possible selectivity of productivity agents. Furthermore, the measure of diversity used as response variable is vital for the outcome of tests of hypotheses on effects of disturbance on diversity. Clearly, there are many aspects to consider in experimental design and interpretation of results in disturbance-diversity studies. Consequently, in order to increase the generality and commensurability among studies, it will be of great benefit if experimenters (i) define the type of disturbance used in the study, (ii) assign ecologically relevant agents of disturbance and productivity with quantifiable components, (iii) recognize the characteristics of the community the disturbance is inflicted upon, and (iv) specify, and justify, the measure of diversity to be used in tests of hypotheses on effects of disturbance on diversity.

References

- Abrams, P. A. 1995. Monotonic or Unimodal Diversity Productivity Gradients - What Does Competition Theory Predict. *Ecology* **76**:2019-2027.
- Abugov, R. 1982. Species diversity and phasing of disturbance. *Ecology* **63**:289 – 293
- Amarasekare, P., M. F. Hoopes, N. Mouquet, and M. Holyoak. 2004. Mechanisms of coexistence in competitive metacommunities. *American Naturalist* **164**:310-326.
- Armesto, J. J. and S. T. A. Pickett. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* **66**:230-240.
- Ayling, A. M. 1981. The Role of Biological Disturbance in Temperate Subtidal Encrusting Communities. *Ecology* **62**:830-847.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation Experiments in Community Ecology: Theory and Practice. *Ecology* **65**:1-13.
- Benedetti-Cecchi, L., F. Pannaciuoli, F. Bulleri, P. S. Moschella, L. Airoidi, G. Relini, and F. Cinelli. 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. *Marine Ecology-Progress Series* **214**:137-150.
- Benmayor, R., A. Buckling, M. B. Bonsall, M. A. Brockhurst, and D. J. Hodgson. 2008. The interactive effects of parasitesf disturbance, and productivity on experimental adaptive radiations. *Evolution* **62**:467-477.
- Berntsson, K. M., P. R. Jonsson, A. I. Larsson, and S. Holdt. 2004. Rejection of unsuitable substrata as a potential driver of aggregated settlement in the barnacle *Balanus improvisus*. *Marine Ecology-Progress Series* **275**:199-210.
- Bertocci, I., E. Maggi, S. Vaselli, and L. Benedetti-Cecchi. 2005. Contrasting effects of mean intensity and temporal variation of disturbance on a rocky seashore. *Ecology* **86**:2061-2067.
- Buckling, A., R. Kassen, G. Bell, and P. B. Rainey. 2000. Disturbance and diversity in experimental microcosms. *Nature* **408**:961-964.
- Canning-Clode, J., M. Kaufmann, M. Molis, M. Wahl, and M. Lenz. 2008. Influence of disturbance and nutrient enrichment on early successional fouling communities in an oligotrophic marine system. *Marine Ecology-an Evolutionary Perspective* **29**:115-124.
- Cardinale, B. J. and M. A. Palmer. 2002. Disturbance moderates biodiversity-ecosystem function relationships: Experimental evidence from caddisflies in stream mesocosms. *Ecology* **83**:1915-1927.
- Caswell, H. and L. A. Real. 1987. An Approach to the Perturbation Analysis of Optimal Life Histories. *Ecology* **68**:1045-1050.
- Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics* **31**:343-366.
- Chesson, P. and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* **150**:519-553.
- Collins, S. L. 1987. Interaction of Disturbances in Tallgrass Prairie - a Field Experiment. *Ecology* **68**:1243-1250.
- Collins, S. L. and S. M. Glenn. 1997. Intermediate disturbance and its relationship to within- and between-patch dynamics. *New Zealand Journal of Ecology* **21**:103-110.
- Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental-Analysis of Intermediate Disturbance and Initial Floristic Composition - Decoupling Cause and Effect. *Ecology* **76**:486-492.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* **199**:1302 – 1310.

- Connell, J. H. and E. Orias. 1964. The ecological regulation of species diversity. *American Naturalist* **98**: 399 – 414.
- Cooper, W. S. 1913. The climax forest of Isle Royale, Lake Superior and its development. *Botanical Gazette* **55**:189-235.
- Cowie, P. R., S. Widdicombe, and M. C. Austen. 2000. Effects of physical disturbance on an estuarine intertidal community: field and mesocosm results compared. *Marine Biology* **136**:485-495.
- Crawley, M. J. 2004. Timing of disturbance and coexistence in a species-rich ruderal plant community. *Ecology* **85**:3277-3288.
- Cruz-Rivera, E. and M. E. Hay. 2000. The effects of diet mixing on consumer fitness: macroalgae, epiphytes, and animal matter as food for marine amphipods. *Oecologia* **123**:252-264.
- Davies, R. G., P. Eggleton, L. Dibog, J. H. Lawton, D. E. Bignell, A. Brauman, C. Hartmann, L. Nunes, J. Holt, and C. Rouland. 1999. Successional response of a tropical forest termite assemblage to experimental habitat perturbation. *Journal of Applied Ecology* **36**:946-962.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**:528-534.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351 – 389.
- Dayton, P. K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community *Ecological Monographs* **45**:137-159.
- Death, R. G. 2002. Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos* **97**:18-30.
- Death, R. G. and M. J. Winterbourn. 1995. Diversity patterns in stream benthic invertebrate communities: the influence of habitat stability. *Ecology* **76**:1446-1460.
- Dial, R. and J. Roughgarden. 1998. Theory of marine communities: The intermediate disturbance hypothesis. *Ecology* **79**:1412-1424.
- Diaz, R. J. and R. Rosenberg. 1995. Marine benthic hypoxia: A review of its ecological effects and the behavioural responses of benthic macrofauna. Pages 245-303 *Oceanography and Marine Biology - an Annual Review*, Vol 33.
- Eggeling, W. J. 1947. Observations on the ecology of the Budongo rain forest, Uganda. *Journal of ecology* **34**:20 – 87.
- Emlen, J. M. 1966. The Role of Time and Energy in Food Preference. *The American Naturalist* **100**:611-617.
- Flöder, S. and U. Sommer. 1999. Diversity in planktonic communities: An experimental test of the intermediate disturbance hypothesis. *Limnology and Oceanography* **44**:1114-1119.
- Fox, J. F. 1981. Intermediate levels of soil disturbance maximize alpine plant diversity. *Nature* **293**:564-565.
- Fuentes, E. R. and F. M. Jaksic. 1988. The Hump-Backed Species Diversity Curve: Why Has It Not Been Found among Land Animals? *Oikos* **53**:139-143.
- Garstecki, T. and S. A. Wickham. 2003. The response of benthic rhizopods to sediment disturbance does not support the intermediate disturbance hypothesis. *Oikos* **103**:528-536.
- Gignoux, J., J. Clobert, and J. C. Menaut. 1997. Alternative fire resistance strategies in savanna trees. *Oecologia* **110**:576-583.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**:344-347.

- Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**:1169 – 1194.
- Guo, Q. F. 1996. Effects of bannertail kangaroo rat mounds on small-scale plant community structure. *Oecologia* **106**:247-256.
- Gutt, J. and D. Piepenburg. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology-Progress Series* **253**:77-83.
- Haddad, N. M., M. Holyoak, T. M. Mata, K. F. Davies, B. A. Melbourne, and K. Preston. 2008. Species' traits predict the effects of disturbance and productivity on diversity. *Ecology Letters* **11**:348-356.
- Horn, H. S. 1975. Markovian properties of forest succession. Pages 196-211 *in* M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press of Harvard University Press, Cambridge.
- Huston, M. A. 1979. A general hypothesis of species diversity. *American Naturalist* **113**:81 – 101.
- Huxham, M., I. Roberts, and J. Bremner. 2000. A field test of the intermediate disturbance hypothesis in the soft-bottom intertidal. *International Review of Hydrobiology* **85**:379-394.
- Jackson, J. B. C. 1977. Competition on Marine Hard Substrata: the adaptive significance of Solitary and colonial Strategies. *American Naturalist* **111**:743 - 767.
- Jara, V. C., J. H. S. Miyamoto, B. A. P. da Gama, M. Molis, M. Wahl, and R. C. Pereira. 2006. Limited evidence of interactive disturbance and nutrient effects on the diversity of macrobenthic assemblages. *Marine Ecology-Progress Series* **308**:37-48.
- Jonsson, P. R., K. M. Berntsson, and A. I. Larsson. 2004. Linking larval supply to recruitment: Flow-mediated control of initial adhesion of barnacle larvae. *Ecology* **85**:2850-2859.
- Kimmerer, R. W. and T. F. H. Allen. 1982. The Role of Disturbance in the Pattern of a Riparian Bryophyte Community. *American Midland Naturalist* **107**:370-383.
- Kneitel, J. M. and J. M. Chase. 2004. Disturbance, predator, and resource interactions alter container community composition. *Ecology* **85**:2088-2093.
- Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. *Proceedings of the Royal Society of London Series B-Biological Sciences* **268**:269-271.
- Lake, P. S., T. J. Doeg, and R. Marchant. 1989. Effects of Multiple Disturbance on Macroinvertebrate Communities in the Acheron River, Victoria. *Australian Journal of Ecology* **14**:507-514.
- Lane, P. A. 1986. Symmetry, change, perturbation, and observation mode in natural communities. *Ecology* **67**:223-239.
- Leclerc, J. 1991. Optimal foraging strategy of the sheet-web spider *Lepthyphantes flavipes* under perturbation. *Ecology* **72**:1267-1272.
- Lenz, M., M. Molis, and M. Wahl. 2004. Testing the intermediate disturbance hypothesis: response of fouling communities to various levels of emersion intensity. *Marine Ecology-Progress Series* **278**:53-65.
- Levin, S. A. and R. T. Paine. 1974. Disturbance, patch formation, and community structure. *Proc. Nat. Acad. Sci. Usa.* **71**:2744 – 2747.
- Li, J., W. A. Loneragan, J. A. Duggin, and C. D. Grant. 2004. Issues affecting the measurement of disturbance response patterns in herbaceous vegetation - A test of the intermediate disturbance hypothesis. *Plant Ecology* **172**:11-26.
- Mackey, R. L. and D. J. Currie. 2000. A re-examination of the expected effects of disturbance on diversity. *Oikos* **88**:483-493.

- Mackey, R. L. and D. J. Currie. 2001. The diversity-disturbance relationship: Is it generally strong and peaked? *Ecology* **82**:3479-3492.
- McCabe, D. J. and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* **124**:270-279.
- McGuinness, K. A. 1987. Disturbance And Organisms On Boulders .2. Causes Of Patterns In Diversity And Abundance. *Oecologia* **71**:420-430.
- Menge, B. A. and J. P. Sutherland. 1987. Community Regulation - Variation in Disturbance, Competition, and Predation in Relation to Environmental-Stress and Recruitment. *American Naturalist* **130**:730-757.
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *American Naturalist* **120**:533 – 536.
- Miyake, Y. and S. Nakano. 2002. Effects of substratum stability on diversity of stream invertebrates during baseflow at two spatial scales. *Freshwater Biology* **47**:219-230.
- Molino, J. F. and D. Sabatier. 2001. Tree diversity in tropical rain forests: A validation of the intermediate disturbance hypothesis. *Science* **294**:1702-1704.
- Mouritsen, K. N. and R. Poulin. 2005. Parasites boosts biodiversity and changes animal community structure by trait-mediated indirect effects. *Oikos* **108**:344-350.
- Odum, E. P. 1963. *Ecology*. Holt, Rinehart and Winston, New York
- Odum, E. P., J. T. Finn, and E. H. Franz. 1979. Perturbation theory and the subsidy-stress gradient. *Bioscience* **29**:349-352.
- Onuf, C. P., J. M. Teal, and I. Valiela. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. *Ecology* **58**:514-526.
- Osman, R. W. 1977. The establishment and development of a marine epifaunal community. *Ecological Monographs* **47**:37 – 63.
- Osman, R. W. and R. B. Whitlatch. 1978. SocietyPatterns of Species Diversity: Fact or Artifact? *Paleobiology* **4**:41-54.
- Pacala, S. W. and M. Rees. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *American Naturalist* **152**:729-737.
- Padisak, J. 1993. The Influence of Different Disturbance Frequencies on the Species Richness, Diversity and Equitability of Phytoplankton in Shallow Lakes. *Hydrobiologia* **249**:135-156.
- Paine, R. T. and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecological Monographs* **51**:145 – 178.
- Pavia, H. and E. Brock. 2000. Extrinsic factors influencing phlorotannin production in the brown alga *Ascophyllum nodosum*. *Marine Ecology-Progress Series* **193**:285-294.
- Peters, R. H. 1991. *A critique for ecology*. Cambridge University Press, Cambridge.
- Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *Quarterly Review Of Biology* **64**:393-418.
- Pickett, S. T. A., J. Kolasa, J. J. Armesto, and S. L. Collins. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos* **54**:129-136.
- Pickett, S. T. A. and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic press, London.
- Proulx, M. and A. Mazumder. 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79**:2581-2592.
- Rapport, D. J., H. A. Regier, and T. C. Hutchinson. 1985. Ecosystem Behavior Under Stress. *American Naturalist* **125**:617 – 640.
- Reynolds, C. S. 1995. The Intermediate Disturbance Hypothesis and its applicability to planktonic communities: Comments on the views of Padisak and Wilson. *New Zealand Journal of Ecology* **19**:219-225.

- Reynolds, C. S., J. Padisak, and U. Sommer. 1993. Intermediate Disturbance in the Ecology of Phytoplankton and the Maintenance of Species-Diversity - a Synthesis. *Hydrobiologia* **249**:183-188.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment Dynamics in Complex Life-Cycles. *Science* **241**:1460-1466.
- Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The intermediate disturbance hypothesis: Patch dynamics and mechanisms of species coexistence. *Ecology* **85**:359-371.
- Rykiel, E. J. 1985. Towards a definition of ecological disturbance. *Australian Journal of Ecology* **10**:361-365.
- Schoener, T. W. 1972. Mathematical ecology and its place among the sciences. I. The biological domain. *Science* **178**:389-391.
- Scholes, L., P. H. Warren, and A. P. Beckerman. 2005. The combined effects of energy and disturbance on species richness in protist microcosms. *Ecology Letters* **8**:730-738.
- Shea, K., S. H. Roxburgh, and E. S. J. Rauscher. 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* **7**:491-508.
- Sheil, D. 2001. Long-term observations of rain forest succession, tree diversity and responses to disturbance. *Plant Ecology* **155**:183-199.
- Sheil, D. and D. Burslem. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology & Evolution* **18**:18-26.
- Sousa, W. P. 1979a. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology* **60**:1225 – 1239.
- Sousa, W. P. 1979b. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecological Monographs* **49**:227-254.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* **15**:353 – 391.
- Sousa, W. P. 2001. Natural disturbance and the dynamics of marine benthic communities. Sinauer, Sunderland, Massachusetts, USA.
- Steneck, R. S., S. D. Hacker, and M. N. Dethier. 1991. Mechanisms of Competitive Dominance between Crustose Coralline Algae - an Herbivore-Mediated Competitive Reversal. *Ecology* **72**:938-950.
- Sugden, H., M. Lenz, M. Molis, M. Wahl, and J. C. Thomason. 2008. The interaction between nutrient availability and disturbance frequency on the diversity of benthic marine communities on the north-east coast of England. *Journal of Animal Ecology* **77**:24-31.
- Sugden, H., R. Panusch, M. Lenz, M. Wahl, and J. C. Thomason. 2007. Temporal variability of disturbances: is this important for diversity and structure of marine fouling assemblages? *Marine Ecology-an Evolutionary Perspective* **28**:368-376.
- Szentkiralyi, F. and F. Kozar. 1991. How many species are there in apple insect communities – testing the resource diversity and intermediate disturbance hypotheses. *Ecological Entomology* **16**:491-503.
- Talbot, F. H., B. C. Russel, and G. R. V. Anderson. 1978. Coral reef fish communities: unstable, high diversity systems? . *Ecological Monographs* **48**:425 – 440.
- Tilman, D. 1980. Resources, a graphical-mechanistic to competition and predation. *American Naturalist* **116**:362-393.
- Tuck, I. D., S. J. Hall, M. R. Robertson, E. Armstrong, and D. J. Basford. 1998. Effects of physical trawling disturbance in a previously unfished sheltered Scottish sea loch. *Marine Ecology-Progress Series* **162**:227-242.
- Turkington, R., E. Klein, and C. P. Chanway. 1993. Interactive Effects of Nutrients and Disturbance - an Experimental Test of Plant Strategy Theory. *Ecology* **74**:863-878.

- Tuytens, F. A. M., R. J. Delahay, D. W. MacDonald, C. L. Cheeseman, B. Long, and C. A. Donnelly. 2000. Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology* **69**:815-828.
- Underwood, A. J. and M. J. Anderson. 1994. Seasonal and Temporal Aspects of Recruitment and Succession in an Intertidal Estuarine Fouling Assemblage. *Journal of the Marine Biological Association of the United Kingdom* **74**:563-584.
- Valdivia, N., A. Heidemann, M. Thiel, M. Molis, and M. Wahl. 2005. Effects of disturbance on the diversity of hard-bottom macrobenthic communities on the coast of Chile. *Marine Ecology-Progress Series* **299**:45-54.
- Webster, J. R. and B. C. Patten. 1979. Effects of Watershed Perturbation on Stream Potassium and Calcium Dynamics. *Ecological Monographs* **49**:51-72.
- Vetaas, O. R. 1997. The effect of canopy disturbance on species richness in a central Himalayan oak forest. *Plant Ecology* **132**:29-38.
- Widdicombe, S. and M. C. Austen. 1999. Mesocosm investigation into the effects of bioturbation on the diversity and structure of a subtidal macrobenthic community. *Marine Ecology-Progress Series* **189**:181-193.
- Widdicombe, S. and M. C. Austen. 2001. The interaction between physical disturbance and organic enrichment: An important element in structuring benthic communities. *Limnology And Oceanography* **46**:1720-1733.
- Wilkinson, D. M. 1999. The disturbing history of intermediate disturbance. *Oikos* **84**:145-147.
- Willby, N. J., J. R. Pygott, and J. W. Eaton. 2001. Inter-relationships between standing crop, biodiversity and trait attributes of hydrophytic vegetation in artificial waterways. *Freshwater Biology* **46**:883-902.
- Wilson, J. B. 1990. Mechanisms for species co-existence: twelve explanations for Hutchinson's 'paradox of the plankton': evidence from New Zealand plant communities. *N.Z. J. Ecol.* **13** 17 – 42.
- Wilson, J. B. 1994. The Intermediate Disturbance Hypothesis of Species Coexistence Is Based on Patch Dynamics. *New Zealand Journal of Ecology* **18**:176-181.
- Wilson, S. D. and D. Tilman. 2002. Quadratic variation in old-field species richness along gradients of disturbance and nitrogen. *Ecology* **83**:492-504.
- Wootton, J. T. 1998. Effects of disturbance on species diversity: A multitrophic perspective. *American Naturalist* **152**:803-825.
- Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem functioning. *Nature* **417**:848-851.

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Flertalet kemiekologiska G-människor har funnits vid min sida där stöttande aktiviteter inte bara inneburit balkongvistande rusdrycksinmundigande, utan även nakenbadande, trolldegsskapande, kemisk analys-assistans, vågmaskinssnickrande, hälsovådliga undervattensaktiviteter, nikotin-snikande, tröstlöst trälletande, fältmässigt Jägermeister shottande och klipptstrands överblickande butterkaksätande. Till detta gäng hör även min kontorssambo som inte bara guidat mej genom hela Honshu och Hokkaido, utan även förklarar för mej obegripliga saker som projektuppföljning i datalagret och elektronisk fakturahantering. I Tjärnö’s begynnelse fanns smålänningar och dalmasar, men även nollåttor, Disney-karakterer och finnar av båda kön. Skåningar, som det finns alldeles för många av, har lyckligtvis befunnits på behörigt avstånd, men som trots detta, och gärna i kombination med en viss smålänning, ständigt lyckas leta upp en och håna ens fiskekunskaper. There has also been a sensei in the underappreciated art of sandwich making, who relentlessly remind me that things are rarely as good as they seem, and his beloved wife who initially adopted me as a second boyfriend, only to leave me heartbroken for Sverker’s southern regions. Eftersom det finns ett oändligt antal oidentifierbara kräk och slemmiga växter i havsdjupen har jag varit helt beroende de barmhärtiga samariterna Elisabet, Anneli, Fredrik P och Hans-G. I stark kontrast till mentala provningar finns en slagsmålsklubb som äger rum på Tjärnö skola varje onsdag, där revben brutits, blåa ögon mottagits och utdelats av Per B, Erik B, Swantje, Greg, Fidde, Micke, Lars, Finn, Petri, Tuuli, Ankan, Erkan, Göran, Gunnar, Henke, Mats, Martin G, Martin S, Malin, Piff, Puff, Erika, Andreas, Anders, Geno, Josefin, Carl-Johan, Johanna,

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