Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance

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Ecosystem resistance to a single stressor relies on tolerant species that can compensate for sensitive competitors and maintain ecosystem processes, such as primary production. We hypothesize that resistance to additional stressors depends increasingly on species tolerances being positively correlated (i.e. positive species co-tolerance). Initial exposure to a stressor combined with positive species co-tolerance should reduce the impacts of other stressors, which we term stress-induced community tolerance. In contrast, negative species co-tolerance is expected to result in additional stressors having pronounced additive or synergistic impacts on biologically impoverished functional groups, which we term stress-induced community sensitivity. Therefore, the sign and strength of the correlation between species sensitivities to multiple stressors must be considered when predicting the impacts of global change on ecosystem functioning as mediated by changes in biodiversity.

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Global change and loss of biodiversity have increased concern over the cumulative impacts of anthropogenic stressors on ecosystems (Sala et al. 2000, Schindler 2001, Hansson and Brönmark 2002). We refer to a stressor as an abiotic or biotic (e.g. introduction of an alien species) variable that exceeds its range of normal variation, and adversely affects individual physiology or population performance in a statistically significant way (Barrett et al. 1976, Auerbach 1981). Natural and anthropogenic stressors can affect ecosystem functioning through changes in biodiversity, especially when ecosystem processes (e.g. primary production) are maintained by only a few species (Tilman 1999, Vinebrooke et al. 2003).

The accelerating rate of biological impoverishment may render ecosystems incapable of compensating for the loss of biodiversity, thereby reducing their resilience to environmental change (Scheffer et al. 2001). For example, local extinction can reduce the probability of tolerant species being present that can maintain ecosystem processes in an increasingly stressful environment (Ives et al. 1999).

Abiotic and biotic stressors usually do not operate independently, but rather often interact to produce combined impacts on biodiversity and ecosystem functioning (Breitburg et al. 1998, Frost et al. 1999, Schindler 2001). Understanding multiple stressors is particularly

challenging when their combined effect cannot be predicted based on evidence from single-stressor studies – i.e. there are interactions that cause non-additive effects (Breitburg et al. 1999, Folt et al. 1999). Stressors are synergistic when their combined effect is larger than predicted from the sizes of the responses to each stressor alone, and antagonistic when the cumulative impact is smaller than expected (Folt et al. 1999).

Multiple stressors have been demonstrated to impact both aquatic and terrestrial ecosystems. For example, the collapse of Caribbean coral reefs can be attributed to an increased vulnerability to hurricanes and diseases following the loss of herbivorous fishes from overfishing (reviewed by Breitburg et al. 1998). Common combinations of stressors in terrestrial ecosystems include increased eutrophication, salinisation, synthetic organic pollutants, and oxidative smog events (Chapin et al. 1993). In northern freshwater ecosystems, three important stressors are anthropogenic acidification, drought events, and depletion of stratospheric ozone, which interact to increase acidity and exposure to DNA-damaging ultraviolet (UV) radiation by reducing concentrations of UV-attenuating dissolved organic carbon (Schindler et al. 1996, Yan et al. 1996).

Given the increasing multiplicity of environmental stressors associated with global change, there is an urgent need to develop a better understanding of the interactive effects of multiple stressors on ecosystems to better predict their responses to a changing environment. Here, we present a conceptual model of how a set of species that contribute to the same ecosystem process might respond to two co-occurring chronic stressors, based on the relatedness of traits that determine the species' tolerance to each stressor.

Effects of multiple stressors on biodiversity: a conceptual model

We begin by evaluating the effects of two stressors on biodiversity as a function of the correlation between the abilities of individuals or species to tolerate each stressor; we call this relationship co-tolerance. Three scenarios may be envisaged in which chronic exposure to each stressor occurs more or less simultaneously (Fig. 1).

The first scenario considers species sensitivities to stressors A and B to be unrelated (Fig. 1A). In this case, elimination of a sub-set of the species pool by either stressor will leave a sub-set of species which is "random" with respect to sensitivity to the other stressor. As a result, one stressor will eliminate a random sub-set of the species that are not eliminated by the other stressor. Here, if stressor A were already present when stressor B occurred, then ecological history (sensu Fischer et al. 2001a) in terms of initial exposure to stressor A would not strongly influence the effect of stressor B on the
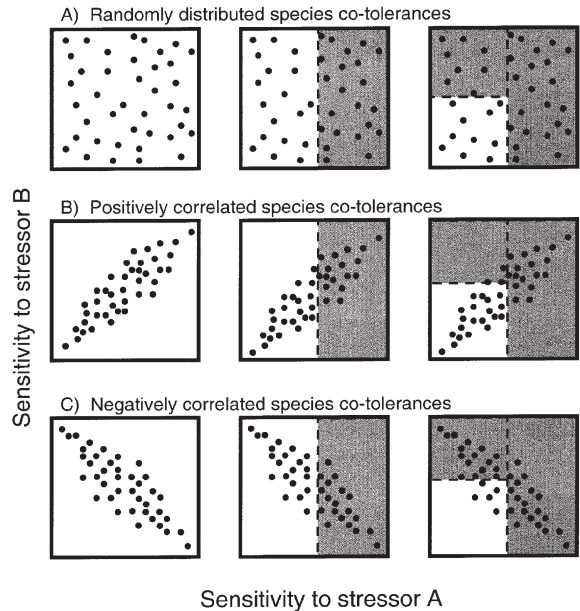

Fig. 1. Hypothetical effects of two stressors on a functional group of 40 species as influenced by the relatedness of their co-tolerances: A) exposure to stressors A (shaded right half) and B (shaded top half) extirpates 20 plus 10 species, resulting in a 75% loss of species when tolerances of each species are randomly distributed; B) exposure to stressor A and B leads to the extinction of 17 plus 3 species, resulting in a loss of only 50% of all species, when tolerances are positively correlated (i.e. stress-induced community tolerance); C) exposure to stressor A and B leads to the extinction of 20 plus 15 species, resulting in a 87.5% loss of the initial species pool when tolerances are negatively correlated (i.e. stress-induced community sensitivity).

relative number of species that are lost. However, sensitivity of a given species to a stressor is not necessarily independent of the presence of another stressor. For example, a species may exist in the presence of either stressor A or B, but not persist in the presence of both. Lack of persistence could result from either a simple additive (i.e. total dose-dependent) or non-additive effect, which would result from a synergistic interaction. Synergy between stressors A and B would result in a greater loss of species than is depicted graphically in our model because it would amplify the effect of one or both stressors, and thereby, expand the boundaries of the shaded areas in Fig. 1. The opposite would apply when the two stressors act antagonistically.

The second scenario occurs when species sensitivities to stressors A and B are positively correlated (Fig. 1B). Here, either stressor eliminates certain species, but leaves more species that are tolerant of the other stressor than if species sensitivities are unrelated (Fig. 1A). Therefore, a positive correlation between species sensitivities (i.e. positive species co-tolerance) increases resistance to one stressor as a result of exposure to the other stressor. We call this stress-induced community tolerance, following the ecotoxicological concept of pollution-induced com-

munity tolerance (PICT) where communities that have been chronically exposed to toxins are relatively less affected by exposure to new pollutants (Blanck and Wängberg 1988). This scenario represents a strong antagonistic interaction between stressors A and B because the former suppresses the effect of the latter, resulting in a combined impact that is less than the sum of their individual effects.

The third scenario occurs when species sensitivities to stressors A and B are negatively correlated (i.e. negative species co-tolerance) because of a trade-off between the traits that determine the ability of a species to tolerate each stressor (Fig. 1C). Here, biodiversity is likely to be severely reduced after both stressors are applied: if one stressor eliminates certain species, then the surviving tolerant species have on average a heightened sensitivity to the other stressor. This is an example of stress-induced community sensitivity, wherein exposure to one stressor synergistically increases the impact of the other stressor as determined by the relative number of species extirpated. However, the cumulative impact of stressors A and B on the absolute number of species lost remains additive because their combined effect approximates the sum of their individual effects (Fig. 1C). Nevertheless, if synergy occurs between stressors A and B, then one or both of their individual effects would increase, which could be depicted in Fig. 1C by expanding the shaded area in our model. Therefore, a synergistic interaction between stressors coupled with stress-induced community sensitivity represents our hypothesized worst-case scenario of maximal species loss.

The location of each point in Fig. 1 representing a species should be viewed as being dynamic, and not fixed. If species sensitivities to stressors are affected by interactions with other species, then species points may move in response to a stressor. For example, the elimination of species by one stressor could release tolerant species from competition, which might better enable them to tolerate other impacts, such as the occurrence of the other stressor. Therefore, competitive release could result in a downward shift into the lower left quadrate of Fig. 1 by certain points as species become less sensitive to either one or both of the stressors. Species tolerances could also show a similar shift during chronic exposure to the stressors because of physiological acclimation, or adaptation by populations that contain intraspecific genetic variation. Conversely, species tolerance may shift towards the upper right quadrant when competition is increased as a result of release of highly competitive species from predation pressure.

Although we have interpreted the symbols in Fig. 1 as species, they could also be used to denote individuals or genotypes within a species. Species do not have fixed physiologies, and stress tolerance depends to some extent on genetic and phenotypic factors that differ among individuals. We expect that correlations between tolerances to different stressors will also occur among individuals of the same species. If the same traits protect against different stressors, a positive correlation arises (Chapin et al. 1993), whereas a trade-off between the traits that cause tolerance to the different stressors will lead to a negative correlation of tolerances. Therefore, points could also be represented by ellipsoids representing individual variability, stretched in the direction of the correlation between traits (Fig. 1).

Implications for ecosystem functioning

We can use our conceptual model to make theoretical predictions about the cumulative impact of multiple stressors on aggregated variables, such as primary production and trophic energy transfer. Evidence from a considerable body of literature suggests that the impact of a stressor is less pronounced at the functional-group-level than at the species-level (Schindler 1990, Howarth 1991, Frost et al. 1995, Cottingham and Carpenter 1998, Vinebrooke et al. 2003). The resistance of aggregate functional variables (e.g. rates of ecosystem processes such as primary production) to environmental stress is usually attributed to compensatory species dynamics: tolerant species succeed competitors that are suppressed or extirpated during a perturbation, thereby maintaining overall ecosystem functioning at the same level (Ives 1995, Klug et al. 2000, Fischer et al. 2001b).

Our conceptual model can be used to make qualitative predictions about the cumulative impact of multiple stressors on ecosystem functioning. The insurance hypothesis (Naeem 1998, Yachi and Loreau 1999) predicts that communities comprised of functional groups with many species results in ecosystem functioning being more resistant to species loss because other tolerant species in the functional group could compensate for the species that have gone extinct because of the stressor (Ives et al. 1999, Yachi and Loreau 1999). However, environmental change often consists of several stressors that can each eliminate certain species that are tolerant of one or more of the other stressors. The compensation effect will critically depend on the sign and magnitude of the species co-tolerance to the different stressors. The loss of species following one stressor may weaken resistance to additional stressors because species that might have been tolerant of the second stressor have been eliminated. Based on our conceptual model, therefore, we predict that ecosystem functioning is more likely to withstand an additional stressor when there is positive co-tolerance than when there is no or negative co-tolerance, because fewer species are lost.

The insurance effect would also be expected to be weakened when species that are important for maintain-

ing a given ecosystem process are similarly sensitive to stressors. Consider the situation when all species in a community that play a similar role are divided into groups, rather than treated equally as in Fig. 1. For example, instead of treating phytoplankton as a homogenous group of primary producers, we can divide them into functional groups based on size, morphology, or physiological parameters (Klug and Cottingham 2001, Reynolds et al. 2002). Division into size classes indicates the probability of consumption by zooplankton and subsequent transmission through the food web, while physiological categories indicate groups of species that perform unique processes such as nitrogen fixation (cyanobacteria) or biogenic opal formation (diatoms and chrysophytes, Reynolds et al. 2002). The likely effects of multiple stressors on ecosystem functioning depend on how tolerances are distributed within and among these functional groups. When functional groups are randomly distributed in tolerance space, there is more scope for compensatory interactions than if species in functional groups have clustered tolerances. However, if species within functional groups have clustered tolerances, entire functional groups may be eliminated when there is negative co-tolerance. This situation has a real world analog: N-fixing cyanobacteria and opal-producing diatoms are extirpated from acidifying lakes in a predictable sequence (Vinebrooke et al. 2003). When these species go extinct, the specific ecosystem process they promote will cease. Importantly, the impact of these losses is likely to be context-dependent; for example, the consequences for overall ecosystem functioning of N-fixer extinction depend on whether N is a limiting nutrient within an ecosystem. Nevertheless, we would expect to see changes in ecosystem functioning when functionally similar species have similar tolerances to stressors, regardless of how the functional similarity is defined.

Ecosystem functioning can also be affected by multiple stressors that alter the size structure within functional groups. There is evidence that smaller species are more often better able to withstand anthropogenic stressors (Odum 1985, Cattaneo et al. 1998, Leech and Williamson 2000). A stress-induced shift towards small species may affect ecosystem functioning in more subtle ways than the loss of entire functional groups. For example, zooplankton communities composed mainly of small species are likely to have lower per capita grazing rates (Peters and Downing 1984) and therefore lower overall grazing rates unless there are corresponding increases in density and biomass. Moreover, because smaller zooplankton are less vulnerable to fish predation (Brooks and Dodson 1965), trophic energy transfer is reduced when smaller zooplankton dominate. Although predation and other biotic processes (e.g. competition) are not typically considered to be stressors, invasion of alien species can cause biotic factors (e.g. predation

pressure) to exceed their range of normal variation, and thereby, function as stressors that narrow the size structure within trophic levels such as the herbivorous zooplankton (Schindler and Parker 2002).

Empirical evidence from aquatic ecosystems

To illustrate the applicability of our conceptual model to real ecosystems, we focus on the expected interactions associated with two common stressors of freshwater ecosystems, namely acidification and human land-use. However, our conceptual model should in principle also apply to other types of multiple stressors and ecosystems.

Anthropogenically acidified lakes provide an excellent example of communities exposed to multiple stressors (Frost et al. 1999), allowing us to explore our conceptual model for several functional groups (Table 1). Acidification typically shifts phytoplankton communities towards larger dinoflagellates and filamentous green algae, while suppressing cyanobacteria and smaller chrysophytes (Klug et al. 2000, Vinebrooke et al. 2003) and larger eukaryotic algae that are less well adapted to higher temperatures (Tilman et al. 1986, Agawin et al. 2000), suggesting that acidification and environmental warming have synergistic negative impacts on phytoplankton. In contrast, ultraviolet radiation has a smaller effect on phytoplankton in acidified lakes than in circumneutral lakes (Xenopoulos et al. 2002), suggesting that there is positive co-tolerance to pH and UV stress as a result of concomitant increases in acidity and declines in UV-attenuating dissolved organic carbon in acidifying lakes (Schindler et al. 1996, Yan et al. 1996).

Since acidification favours smaller zooplankton species, such as rotifers and certain copepods (Frost et al. 1995, Fischer et al. 2001b, Vinebrooke et al. 2003), we hypothesize that the effects of several other stressors on zooplankton will be reduced in acidified lakes. For example, smaller zooplankton species experience lower metabolic costs per capita than larger ones during warming events (Moore et al. 1996, Folt et al. 1999). Similarly, smaller zooplankton are less vulnerable to UV radiation (Leech and Williamson 2000), visually feeding vertebrate predators (Brooks and Dodson 1965, Gliwicz 2002), and pesticides (Moore and Folt 1993, Hanazato 1998).

In contrast, for certain planktonic crustaceans we would expect acidification to amplify the effects of UV radiation and predation pressure. For example, copepod species that are both acid- and UV-tolerant because of their capacity to produce photo-protective pigmentation are likely to face an increased risk of predation by visually-feeding planktivorous fish (Hansson 2000), especially if large populations of alien sportfish are introduced into clear lakes (Donald et al. 2001, Schindler

Table 1. Hypothesized antagonistic (+) and synergistic (−) effects of anthropogenic acidification (stressor A) and other major abiotic and biotic stressors (stressor B) on phytoplankton and zooplankton.

Stressor B	Phytoplankton	Zooplankton	Rationale
Elevated temperature	−	+	Acid-sensitive cyanobacteria are thermophilic[1]; small acid-tolerant zooplankton (e.g. rotifers) experience lower metabolic costs than large acid-sensitive cladocerans[2].
Ultraviolet radiation	+	+	Acid-tolerant species must also be UV-tolerant as they experience elevated UV exposure during lake acidification and loss of UV-attenuating dissolved organic carbon[3]. Small acid-tolerant rotifers show higher UV tolerance than other zooplankton[4].
Eutrophication	−	?	Acid-sensitive cyanobacteria are better competitors for nutrients than other groups of phytoplankton[5].
Toxins	+	+	Acid-tolerant, small zooplankton species are more resistant to contaminants than large ones[6].
Predation	+	−	Large acid-tolerant phytoplankton (e.g. cyanobacteria, dinoflagellates) are less edible; smaller zooplankton are more susceptible to predatory invertebrates like *Chaoborus*, while pigmented UV- and acid-tolerant zooplankton are easily detected by introduced fish[7].

[1]Tilman et al. 1986, Agawin et al. 2000, Vinebrooke et al. 2003; [2]Moore and Folt 1993, Moore et al. 1996; [3]Schindler et al. 1996, Yan et al. 1996, Xenopoulos et al. 2002; [4]Leech and Williamson 2000; [5]Tilman et al. 1986, Vinebrooke et al. 2003; [6]Moore and Folt 1993; [7]Brooks and Dodson 1965, Williamson et al. 1999, Hansson 2000, Donald et al. 2001, Fischer et al. 2001b, Schindler and Parker 2002.

and Parker 2002). Subsequently, smaller acid-tolerant species are more susceptible to large predatory invertebrates (e.g. *Chaoborus*), which become more abundant in lakes once they have become severely acidified and rendered fishless (Williamson et al. 1999, Fischer et al. 2001b). However, acidification can also amplify the effects of UV radiation on the acid-tolerant, predatory phantom midge *Chaoborus* because it lacks photoprotective pigmentation (Williamson et al. 1999). Finally, adverse impacts of increased UV exposure on acid-tolerant zooplankton may be offset by environmental warming because photorepair is enhanced by higher water temperatures (Williamson et al. 2002).

A number of stressors can also affect functional groups in ecosystems that are influenced by changes in land-use. For example, eutrophication and pesticides are major stressors affecting agricultural environments (Smith 1998), while urban systems are often impacted by high salinity (Kolpin et al. 2002). Morphological and life-history traits of zooplankton adapted to eutrophic environments and elevated pesticide levels are probably positively correlated (Gliwicz et al. 1981) since their ability to survive either stressor depends on fast reproduction and small body size (Moore and Folt 1993). Accordingly, zooplankton communities stressed by pesticides are indeed dominated by rotifers and small crustacean species (Hanazato 1998). In contrast, reproductive rate is inversely related to species tolerance of high salinity, probably because of energy allocation to osmoregulation (Harris and Aladin 1997). Thus, we expect that the adaptive traits for tolerance of eutrophication and pesticide exposure in lakes situated in agricultural catchments are negatively correlated with traits for salinity tolerance in urban lakes. As a consequence, functional groups that have been previously exposed to agricultural stressors may exhibit

stress-induced community sensitivity and be especially sensitive to the impacts of future urban development.

Conclusion

Our conceptual model shows that the sign and strength of correlations between stressor tolerances affect the response of biodiversity and ecosystem functioning to multiple stressors. Species traits that determine the tolerance to one chronic stressor can influence how communities and functional groups respond to other stressors. For example, a stressor-induced shift towards smaller species may represent a generalized stress response (sensu Chapin et al. 1993) that can be acted upon by natural selection, further strengthening positive co-tolerance among taxa. In contrast, lack of previous exposure and adaptation to specific combinations of stressors is expected to decrease the probability of species within a functional group exhibiting positive co-tolerance, thereby reducing resistance. The potential influence of past events on the development of species co-tolerance highlights the importance of ecological history in predicting responses to environmental change (Fischer et al. 2001a), and suggests that novel combinations of stressors may have particularly serious consequences for biodiversity and ecosystem functioning.

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