
Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes

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Changes in environmental conditions often reverse outcomes of competitive interactions among species. Such context dependency implies that the speed, persistence, and ubiquity of anthropogenic habitat alterations may suddenly put even previously well-adapted native species at a competitive disadvantage with non-native species. That is, anthropogenic disturbance may so drastically alter environments that a native species finds itself in an environment that in key ways is just as novel as it is to a non-indigenous species. Extreme disturbances may thereby erase a native species' prior advantage of local environmental adaptation accrued during its long-term incumbency over evolutionary time. I document examples from two areas of dramatic human alteration of selection regimes – eutrophication and the selective removal of top predators – that support this mechanism. Additionally, I highlight ways in which this mechanism is experimentally testable. Alteration of selection regimes may prove to be a powerful explanation for the enhanced success and impact of biological invasions in our globally disturbed biosphere.

Interactions with non-indigenous species have been identified as one of the leading causes of endangerment and extinction of native species (Czech and Krausman 1997, Wilcove et al. 1998). Competition in particular is increasingly recognized as a major means through which non-indigenous species impact and displace native species (Settle and Wilson 1990, Petren and Case 1996, Kupferberg 1997, Juliano 1998, Byers 2000a). These findings, however, raise a fundamental question: How does a non-indigenous species in a novel environment gain competitive advantage over a resident species that has supposedly been honed to that environment for thousands of years? Well-adapted native species would usually be expected to have a marked competitive advantage over newly arriving species that are adapted to different habitats and resource availabilities (Vermeij and Dudley 2000). In fact, the concept of competitive advantages inherently favoring native species is seemingly widespread and commonly acknowl-

edged in the ecological literature under a variety of terms, e.g. home-field advantage, prior resident effect, or priority effect (Case 1991, Pimm 1991, Massot et al. 1994).

Here I argue that, at least in part, the answer may stem from rapid anthropogenic alteration of selection regimes. Humans are dramatically altering habitats and food web structures (Vitousek et al. 1997), causing profound environmental changes. These changes often transform a system on time scales as fast as years or even days, and are thus much faster than the evolutionary responses of native species. If such rapid anthropogenic alteration skews the environmental conditions to which a native species was well adapted, the native species may lose its prior advantage over non-indigenous species in context-dependent interactions like competition. Because of the influx of many non-indigenous species to most ecological systems, the odds are often good that at least one of these invading species will by chance possess traits that allow it to perform relatively better in the changed environment than the resident species. In other words, extreme anthropogenic disturbances may create a mismatch between traits of native species and their environment, so that some invading species are as well, if not better, adapted to the altered environment than competing native species.

Throughout this paper I use the term selection regime modification (SRM) to refer specifically to severe, anthropogenically induced disturbances that are outside the magnitude, duration, or frequency of natural disturbances that occasionally affect systems. Thus, I use the term SRM to imply the sudden introduction of a strong selective force that is substantially different than any that would have been experienced by a resident species in its evolutionary history. Certainly invasion success can be influenced by factors unrelated to

disturbance, e.g. the supply rate of non-indigenous propagules (Carlton and Geller 1993). However, there is a vast literature documenting the common association between biological invasions and anthropogenically disturbed habitat (Rejmánek 1989, Bossard 1991, Hobbs 1991, Appleby 1998, D'Antonio et al. 1999, Dukes and Mooney 1999). This paper is not intended as a thorough review of that literature; however, in general, three explanations have emerged from such studies to explain the common coupling of disturbance and invasion (although they are seldom experimentally examined). 1) Disturbance creates new microhabitats and niches for invading species (Parker et al. 1993, Carlton 1996, 2000). 2) Disturbances directly remove or decrease populations of native predator and competitor species, thereby making them less capable of controlling or resisting a growing population of invading species (D'Antonio 1993, Moyle and Light 1996, Kotanen 1997, Stylinski and Allen 1999, Davis et al. 2000). 3) Disturbance agents introduce non-indigenous species' propagules into areas that were inaccessible to the propagules on their own (Usher 1988, Lonsdale 1999).

The emphasis of these explanations has been primarily to account for the increase in the frequency of successful invasions over the last hundred years. The SRM mechanism I advocate – that anthropogenic disturbances often sufficiently alter environments to create competitive advantages for non-native species over native species – shares this emphasis, but also accounts for the displacement of native species through interactions with non-indigenous species after disturbance. That is, it also predicts that severe disturbance will on average increase the impact of non-indigenous species on native species. Selection regime modification has been implicit in some of these previous explanations. Here I make this mechanism explicit by viewing the effect of disturbance on invasion from the native species' perspective. To this end I hope not only to focus more attention on a hypothesis that may mechanistically explain how non-indigenous species exert such strong impacts on native species, but also to produce useful tests and predictions. Although intuitively appealing, evidence from the literature to support the SRM mechanism is seemingly sparse; here I discuss some of the better examples.

Testing the selection regime modification mechanism

Two approaches to testing the mechanism are readily apparent. First, some key environmental variable that influences competitive ability or mortality rates within the recipient habitat can be shown to have changed so that it is now more similar to the source habitat of the invader than to the pre-disturbance habitat of the native species. Second, a disturbance-induced change in

an environmental variable in the recipient habitat can be experimentally shown to be responsible for an invader's advantage over a native species. While the second approach is more detailed and requires experimental documentation, all of the supporting examples I present test the mechanism this way. The lack of studies using the former test is hardly surprising given the frequent difficulty in getting good data on non-indigenous species in their native environments, and also because of the hard or impossible task of retrieving data on pre-disturbance environmental conditions after a disturbance has occurred. Better baseline data would improve our ability to explore the displacement mechanism using this approach. Support via either of these approaches would indicate that a disturbance had altered the environment to favor the invading species at the expense of the native species. To be sure, data have been collected that compare the performance of an invasive species in its native and introduced habitats (e.g. Lohrer et al. 2000). However, such performance data have not been examined in the context of how they are influenced by disturbance, let alone compared against a native competitor species' fitness before and after disturbance.

As aforementioned, the SRM mechanism also produces a testable prediction – that impact of invading species on native species should be greater in environments receiving anthropogenic disturbance versus environments experiencing only the natural disturbance regime. Preliminary results of a meta-analysis of invasive species provided mixed support for the SRM mechanism, showing that impacts of invaders on native species were smaller in anthropogenically disturbed than undisturbed areas on *population* level parameters, while impacts were greater in disturbed areas when measured on *individual* parameters (Wonham et al. 2000). Although such tests of this prediction can compare impacts in disturbed and undisturbed environments, unless impacts are experimentally demonstrated, the tests are less convincing since they are confounded by the direct impacts of the disturbance itself on native species. A few comparative studies, however, have cogently compared invasive species' impact on natives in neighboring disturbed versus undisturbed environments (Brooks 1995, Kato et al. 1999). I found only one experimental test of this prediction, but it helps to set the framework for how experiments to address this prediction can be effectively conducted. Gould and Gorchov (2000) compared the relative impacts of an invasive shrub, *Lonicera maackii*, on the fecundity and survival of native plant species in two Ohio forest stands – one with almost no anthropogenic disturbances for the last 80 years and the other with a long history of grazing, logging, and fire. They found that experimental removals of the non-indigenous shrub in the disturbed environment greatly increased native plant survival, while removal of the invader in the less

disturbed plots had no effect on native plant survival. (To control for residual effects of the shrubs' presence (alleopathy, alteration of soil nutrients, etc.) and effects of the removal process per se the authors conducted removals well in advance of the experimental measurements and included a reference treatment where *Lonicera maackii* was originally absent.) Thus, their study supports the prediction of the SRM hypothesis – that impact of invaders on native competitors will be stronger in anthropogenically disturbed environments.

Extreme examples provide a heuristic perspective to glean the potential extensiveness of the SRM mechanism. In simplest form, intense anthropogenic disturbances may remove native species that do not tolerate disturbance well, allowing certain invaders to simply fill the vacated niche. In such cases an invader may experience little to no biotic resistance to its establishment from native species. The paleontologic record suggests that successful establishment of non-indigenous species followed catastrophic events in recipient habitats, and that this was the common means by which invasions (i.e. range expansions) succeeded historically (Vermeij 1991). On an ecological time scale disturbances like acid rain may be so severe that many native species are decimated (e.g. Peterson 1982, Stephenson et al. 1995), and the selection regime altered such that only acid-tolerant species can fill the open niche (Malcova et al. 1998). Mack (1986) has argued that native tussock grasses throughout the world are very sensitive to trampling, primarily because they did not evolve with large grazers. Where humans have introduced large herbivores the grasses become trampled and non-native grasses sweep readily into the denuded habitat. Similarly, several authors have suggested that major floods within San Francisco Bay estuaries (exacerbated by human land use patterns) removed freshwater intolerant competitors of introduced shad, striped bass, and an Asian clam (*Portamacorbula amurensis*), enabling their explosive invasions (Hedgepeth 1979, Nichols et al. 1990). The invasion of the non-indigenous ctenophore, *Mnemiopsis leidyi*, to the Black Sea appears now to have been facilitated by extreme levels of overfishing of planktivorous fish, the main competitors of *Mnemiopsis* (Shiganova 1998). Finally, extensive overfishing of the American lobster, *Homarus americanus*, in New England in the late 1800's (Rathburn 1887) is thought to have greatly relaxed predation pressure on the introduced snail, *Littorina littorea*, thereby facilitating its spread throughout the Northeastern US (Vermeij 1982).

Most anthropogenic disturbances, however, do not have such extreme, direct impacts on native species. More commonly, disturbances do not entirely eradicate a native species, but rather skew environmental conditions that once potentially allowed its optimal performance, thereby making it susceptible to displacement by a better performing competitor. I provide examples

from the literature that support the hypothesis that altered selection environments promote competitive displacement of native species by non-native species by focusing on two examples of ubiquitous anthropogenic disturbances. First, I discuss how a dramatic increase in eutrophication has altered aquatic selection environments that in some cases favor non-native species over natives. Second, I discuss how the accentuated loss or addition of top predators in a system, through both direct and indirect means (e.g. habitat fragmentation), may sharply skew the net benefits of anti-predator traits, leaving native species poorly adapted to the current environment. Consequently, changes in the number and diversity of top predators may substantially influence outcomes of predator-mediated competition between non-indigenous and native species.

Example 1: eutrophication effects

Globally, eutrophication is increasing in intensity, frequency and duration in coastal marine and freshwater systems (Officer et al. 1984, Elmgren 1989, Cooper and Brush 1991, Parker and O'Reilly 1991, Iversen et al. 1998). Pronounced eutrophication of aquatic environments often triggers dramatic switches to alternative stable states (Scheffer et al. 2001). These environments have also been some of the most degraded over recent time, e.g. a 90% wetland loss in California over the past 200 years (National Research Council 1992). With the growing ubiquity of eutrophication, plant species that are good competitors at high nutrient levels and animal species that are tolerant of associated low O₂ conditions are likely to be at a competitive advantage. While high nutrient, low O₂ conditions do not inherently favor non-native species over natives, if, for example, a native species was adapted to a consistently high O₂ environment, eutrophication could decrease its fitness, making it vulnerable to competitive displacement by a less oxygen-sensitive invader. While a native species in such an area could still maintain incumbent advantages regarding other aspects of the environment, the overriding influence of oxygen in important stages and interactions of many aquatic species could make it a key determinant (Breitburg et al. 1999). Eutrophication and invasion do seem often to go hand in hand (Koonce et al. 1996, Madsen 1998, Schnitzler and Muller 1998, Byers 2000b), but causality is often hard to show due to the mix of alterations that occur in eutrophic environments. Generalities, however, are emerging from correlative studies in a variety of systems.

In recent years Lake Balaton in central Europe has undergone massive fish kills attributable to eutrophication, yet non-indigenous species biomass has been increasing through even the most extreme anoxic events (Biro 1997). Using the weight of commercially caught

fish as an index, non-indigenous species biomass (5 species) rose from 5% in 1980 to over 60% in the mid-1990's. The increasing incidence of low O₂ conditions therefore seems to be aiding the displacement of native fish species that are known to compete with the introduced species. Also, Schnitzler and Muller (1998) reported that eutrophication in European alluvial floodplains, coupled with damming and other factors, benefited two non-indigenous knotweeds (*Fallopia* sp.). They found that competition with native species in less disturbed settings slowed the spread of the invasion, suggesting that the eutrophic conditions may in part enhance *Fallopia*'s competitive dominance over native plant species. To effectively mitigate the invasion in disturbed areas Schnitzler and Muller suggested that the floodplain be restored to its natural nutrient and flow conditions.

As another example, several globally successful non-indigenous submerged aquatic plants (*Hydrilla*, *Myriophyllum*, *Trapa*) are commonly associated with eutrophic conditions. Ruiz et al. (1999) suggest that these invaders are competitively dominant over native flora because their growth and physiology are well suited to the low light conditions associated with algal and microbial blooms that occur with eutrophication. Finally, Madsen (1998) examined the relationship between the dominance of introduced Eurasian milfoil, *Myriophyllum spicatum*, over native aquatic plants that declined sharply in the presence of milfoil. Using a number of environmental correlates in more than 100 US lakes he found that total phosphorous was the best predictor of dominance (the proportion of littoral zone occupied) by this invasive plant. Regulating lake P concentrations may therefore be an important management tool in controlling the impact of exotic milfoil populations on native species.

Experimental evidence to support the ability of eutrophication to facilitate either the incidence, speed, or impact of non-indigenous species invasion is conspicuously lacking. One example from my own studies implies an effect of eutrophication on the ultimate speed of a native species' displacement by a more robust non-indigenous competitor. I examined the displacement of a native species mudsnail, *Cerithidea californica*, by the invasive mudsnail, *Batillaria atramentaria*, in the highly modified salt marsh habitats of northern California (Byers 1999, 2000a, b). I compared snail mortality under natural field conditions for three summers (Byers 2000a) and under low oxygen conditions (1 µg/ml) in the lab (Byers 2000b). Under both normal and low O₂ concentrations *Batillaria* survived much better than its competitor (Fig. 1). Due to *Cerithidea*'s pronounced mortality under low O₂ conditions the difference in mortality rates between the species was more than an order of magnitude greater compared to normal O₂ conditions. A model parameterized from field data under normal O₂ conditions demonstrated

that the speed and success of *Batillaria*'s invasion and displacement of *Cerithidea* depended primarily on differences in mortality rates between the snails (Byers and Goldwasser 2001). Given the sensitivity of *Cerithidea*'s displacement to mortality rates, the substantial spike in its mortality due to common, although spatially limited, hypoxic events creates a greater discrepancy in the relative mortality of the two species and would hasten the speed of *Batillaria*'s displacement of *Cerithidea*.

Example 2: alteration of apex predation abundance

Anthropogenic alterations can permanently alter the relative abundance of species, which in turn affects food chain dynamics and community interactions (Chapin et al. 1997). These changes therefore drastically

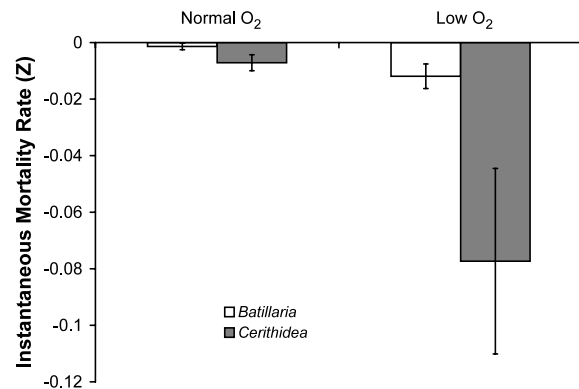


Fig. 1. The weekly per capita instantaneous mortality rate (\pm se) for adult snails under different oxygen conditions. "Normal" represents field mortality measured over 5 $\frac{1}{2}$ to 8 $\frac{1}{2}$ weeks at dissolved oxygen concentrations \sim 4–5 mg/l ($n = 3$ for each species with a range of 486–1483 snails per trial) (Byers 2000a). (Oxygen levels in these experiments were not experimentally controlled, but rather represent natural, ambient levels.) Low oxygen conditions were obtained in laboratory experiments exposing snails to oxygen concentrations \sim 1 mg/l for 4 and 6 weeks (Byers 2000b). For *Cerithidea*, $n = 4$ with 95, 102, 133, 139 snails per trial; for *Batillaria*, $n = 2$ with 134 and 143 snails per trial. Instantaneous mortality rates (Z) were calculated using the standard equation: $N_t = N_0 \times e^{-Zt}$, where N_0 is the number of organisms at time = 0; N_t is the number of survivors at time = t ; t is the number of weeks of the experiment; and Z is the weekly instantaneous rate of mortality. While all O₂ trials were performed over similar time frames, with this standardization, the snails' mortality rates could be compared independent of the exact duration of exposure to their O₂ treatments. A two-way ANOVA on arcsine squareroot transformed values of Z showed that the effects of Species and O₂ were both significant (Species: $F_{1,8} = 7.9$, $P = 0.02$; O₂: $F_{1,8} = 8.9$, $P = 0.017$), while the O₂ \times Species interaction term was not ($F_{1,8} = 1.53$, $P = 0.25$). Although the interaction was not statistically significant (likely due to low replication), the mortality differential was an order of magnitude larger between the species under low O₂ (0.065) compared to normal O₂ (0.0058), suggesting that replacement of the native snail by its competitor would occur more quickly in a low O₂ environment.

alter selective pressures on anti-predator traits of species at lower trophic levels. Changes to community webs can be direct (e.g. overfishing, overexploitation), since human fishing and hunting pressures tend to selectively remove higher trophic levels (Hoogweg et al. 1991, Botsford et al. 1997). Additionally, the removal or reduction of keystone species (which are often top predators), by definition, dramatically affects the remaining ecosystem (Paine 1966, Estes and Palmisano 1974, Berger et al. 2001). Changes to community trophic structure can also be indirect, e.g. through habitat destruction (Dudgeon 1995, Misenhelter and Rotenberry 2000). Fragmentation of habitat due to roads, power lines, or pipelines not only influences population dynamics, gene flow, and home ranges (e.g. Doak 1995), but also differentially affects species within a community, tending to remove most quickly the top carnivores, which typically have the greatest space requirements (Brashares et al. 2001, Terborgh et al. 2001). The accelerated loss of higher trophic levels due to habitat destruction rapidly decreases the per capita predation risk for lower trophic levels (Lovejoy et al. 1984, Bascompte and Sole 1998, Davies et al. 2000).

Certain human modifications to the environment may also increase the abundance of particular predator and parasite species, which may have equally profound effects on selection regimes of prey species. For example, garbage dumps and power lines (used as hunting perches) have increased food availability of ravens, crows, and eagles and led to increases in their populations (Soulé 1990, Boarman and Coe 2000). Opportunistic species can thrive and increase in urban environments (e.g. opossums, skunks, raccoons, cowbirds) and spread into neighboring natural environments (Wilcove 1985, Gates and Evans 1998, Heske et al. 1999). Human activities may also alter prey or predator behavior that increases predation pressure (Post et al. 1999, James and Stuart-Smith 2000). For example, caribou restricted by oil pipelines suffered increased wolf attacks (James and Stuart-Smith 2000).

On an evolutionary time scale physical, chemical, developmental, and behavioral anti-predator traits develop in response to natural selection imposed by predators. Over thousands of years the anti-predator responses should in most cases be fairly well adapted to the predatory selection regime (Vermeij 1987). However, rapid and often permanent changes to a strong selective force like predation, such as those illustrated above, can quickly create a mismatch between a native species' anti-predator traits and local predator abundance and diversity. Specifically, degradation of the predatory regime may dramatically increase the cost/benefit ratio of anti-predator traits, thereby eliminating a native species' prior advantage in predator-mediated competition with an invading species (Fig. 2). That is, native prey that have co-evolved their defenses with predators may be at a disadvantage in competition with

an invasive species if the predator is removed. Given a large amount of time the native species could begin to adapt to the new reduced-predation environment by decreasing investment in anti-predator traits. However, the fast and continuous transport of a high diversity of non-indigenous propagules around the globe greatly increases the probability that a non-indigenous competitor species already investing in defense at a level better suited to the altered environment will arrive long before the native species can evolve to the new optimum. A less defended morph could invade and compete strongly because it is more efficiently designed for the current reduced-predation environment, allocating less of its limited energy to less-essential predator defenses and more to growth and reproduction (Blossey and Notzold 1995, Siemann and Rogers 2001).

In general, fitness costs of anti-predator responses are pervasive (Skelly 1992, Tollrian 1995, Peckarsky and McIntosh 1998, Lagergren et al. 2000). The occurrence of inducible anti-predator traits in some species, where traits do not develop unless prompted by proximate cues of a predator's presence, emphasizes that such traits may be costly to otherwise develop or maintain. For example, Van Buskirk (2000), although he does not address non-indigenous species, evidences the loss in fitness due to development and maintenance of anti-predator traits in anurans when they were experimentally exposed to, yet protected from predators. Specifically, he showed that significant fitness costs arose from exposure to predators due to shifts in the prey's allocation of time and energy to defensive traits. Because of energy limitation, enemy defense for most species is only achieved by diverting resources away from functions such as growth and reproduction (Karban and Baldwin 1997), especially if construction or maintenance costs are associated with the defense structure (Lively 1986, Clark and Harvell 1992). To address the SRM mechanism the best defense traits to study should be constitutive, highly heritable, and costly to produce and maintain (Struhsaker 1968, Pollard 1975). Several potential examples of such anti-predator traits that are also objective and easily quantifiable include spines, chemical defenses, or shell thickness (e.g. Tucker et al. 1997).

Surprisingly, despite the strong potential for changes in the predation environment to influence the impact of invading species on native species, this has seldom been experimentally demonstrated. Several studies though have examined how native predators play a large role in controlling the invasion and establishment of non-indigenous species (Robinson and Wellborn 1988, Baltz and Moyle 1993, Garvey et al. 1994, Reusch 1998, Hill and Lodge 1999, Byers 2002). For example, a non-indigenous mussel (*Musculista senhousia*) forms dense beds and modifies habitat in areas of San Diego Bay. Reusch (1998) demonstrated biotic resistance to the mussel's invasion by a native snail that reduced *Mus-*

Optimization of Anti-Predator Trait

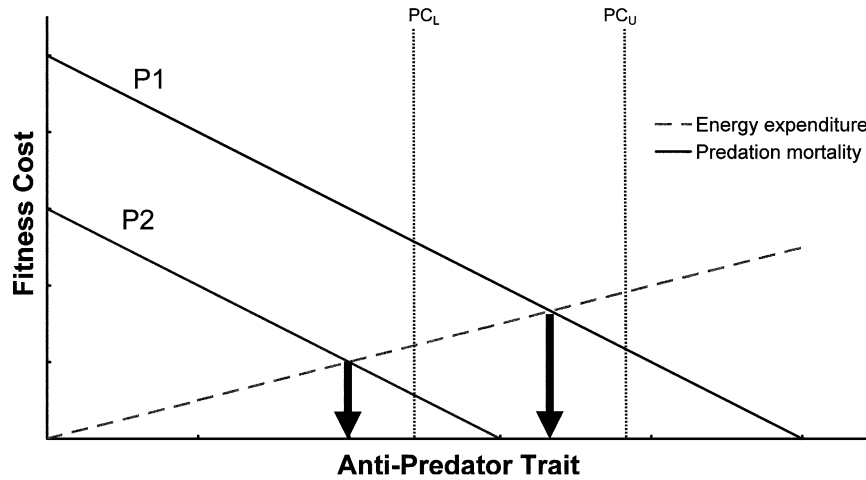


Fig. 2. The optimization of an anti-predator trait in two different predator environments. Moving right along the x-axis represents increasing sophistication, development, or quantity of an anti-predator trait. The fitness cost to a species due to predation mortality and energy expenditure is a function of investment in the anti-predator trait. Assuming energy is limited, the energy cost of constructing and maintaining an anti-predator trait, depicted by the increasing dashed line, reflects the increasing allotment of energy away from other fitness components such as reproduction as the trait is enhanced. In contrast, the fitness cost due to the risk of predation decreases with the level of investment in the trait. The predation risk line P1 (with larger y intercept) represents an environment with higher average predation. The predation line P2 represents an environment where predation pressure has been substantially reduced. For this illustration I assume the organism pays the higher of the two fitness costs for a given value of the anti-predator trait, i.e. fitness cost is minimized and the anti-predator trait is optimized where the predation risk and energy cost lines intersect (marked by the bold arrows). In this example, a sudden sustained drop in predation pressure (i.e. from P1 to P2) would decrease the optimum level of anti-predator trait from the right arrow to the left. The dotted vertical lines (PC_L , PC_U) represent hypothetical lower and upper phylogenetic constraints on an anti-predator trait of a species that evolved in the P1 predator environment. If the predation environment changes substantially, even given unlimited time these constraints may severely restrict a species' ability to achieve a given optimal level of anti-predator trait.

culista populations up to 65% within 2 weeks. Furthermore, the snail favored *Musculista* in feeding trials more than 4.5 times over a native clam species, potentially alleviating competitive stress on the native species. Also, Byers (2002) quantified predation rates of native crabs on the introduced clam, *Nuttallia obscurata*, at >60% in a 24 hour period when the clams were placed on a mud substrate. *Nuttallia*'s only refuge from high predation levels was in loosely packed, sandy substrate found high in the intertidal zone where it was able to bury sufficiently deep to avoid excavating crabs. This refuge likely reduces competition for space between *Nuttallia* and native clam species, which because of their thicker shells and better burial capabilities, inhabit areas lower in the intertidal where crabs, and also food, are more abundant. Findings such as these suggest that there are situations where native species may be particularly susceptible to large impacts if the native predators were lost. Conversely, Garvey et al. (1994), in one of few experimental examinations of a predator's presence/absence on consequent impact, demonstrate that native predators actually heighten the impact of in-

vaders on competing native species. Specifically, when shelters were experimentally limited and predatory fish were present, a native crayfish species was excluded from the shelters by two more aggressive invading congeners and consumed at a high rate.

Finally, anthropogenically spread non-indigenous species may sometimes themselves be viewed as a disturbance that can alter the abundance of top predators, heightening consequent impact on native species. For example, Courchamp et al. (2000) modeled an interesting scenario of apparent competition using realistic parameter estimates where non-indigenous predators (feral cats) fed upon native prey species (birds). Non-indigenous rabbits, which are an alternative prey for cats, but which have been exposed to cats over their evolutionary history (and thus were behaviorally better adapted to avoid predation by cats), were introduced to the simulations. Because the cats could now be partially supported on rabbits as an alternative food source, the rabbits increased the predator population, which exacerbated the impact of the cats on the bird species, and ultimately induced the extinction of the indigenous bird species.

Conclusions

A new selection regime created through drastic environmental alterations could favor a competitor species with a completely separate evolutionary history. Because of severe anthropogenic changes to selective environments, possession of a disparate evolutionary history may actually be advantageous. Habitats that become drastically altered may be more hospitable to species that evolved elsewhere if the altered area more closely resembles the selective environment of the non-indigenous species than it resembles the habitat that shaped the native species. Furthermore, non-indigenous species, especially so-called 'ecosystem engineers' or 'transformers' that substantially modify physical elements of their environment (e.g. hydrology, fire frequency, erosion rates) may themselves disturb and change the selective environment (Vitousek and Walker 1989, D'Antonio and Vitousek 1992, Gordon 1998, Mack and D'Antonio 1998, Dukes and Mooney 1999, Simberloff and Von Holle 1999). In this manner, non-indigenous species may themselves increase and intensify impacts of other invading species.

Inoculations of non-indigenous species and anthropogenic environmental alterations occur on a time scale of hours to years. With the exception of bacteria and similar microorganisms, evolution of species' properties and traits discussed here is likely to take on the order of dozens, if not hundreds of years (but see Carroll and Dingle 1996, Reznick et al. 1997). The disparity in the time scales underscores the inability of native species to respond adequately. Phenotypic plasticity is well documented for anti-predator traits of a variety of taxa and may allow a species to respond on a shorter time scale to anthropogenic disturbances than genetic changes would otherwise allow (e.g. Trussell and Smith 2000). However plasticity, while faster, has more defined limits on the alterations that are possible, and may not be a physiological possibility for all species or for all traits.

Future tests of the effects of disturbance on invasion success and native displacement should further address the SRM mechanism discussed here. With some ingenuity it should be testable on short time scales. For example, this mechanism could be studied through experiments that factorially manipulate disturbance and the presence of introduced competitors to track the relative performance of the native and non-indigenous species. If target species are too long-lived for experiments to extend to complete exclusion, the experiments could quantify whether the native species exhibits lower relative fitness in the presence of introduced competitors after disturbances. Alternatively, invading species can be removed from paired disturbed and undisturbed plots to examine performance consequences for native species. The SRM mechanism predicts that removal of non-indigenous species from disturbed areas will produce greater positive effects on fitness of native species

than similar removals in undisturbed areas. Systems under ecological restoration may be a ripe source for studying this issue. Specifically, the impact of non-indigenous species on native species should lessen as the system recovers from a disturbed state to its more pristine or historical state. The impact of non-indigenous species on native species could therefore be monitored in systems under restoration and compared to non-restored control sites. However, in such cases the researcher must be able to control for improvements in the native species' performance due to direct effects of the system's recovery, perhaps with a second control area under restoration but with no invader present.

Ultimately, species invasions are influenced by anthropogenic disturbances. These disturbances increase invasion success not only by creating new microhabitats, introducing propagules, and decreasing populations of native species that can resist invasion, but also, as I advocate, by weakening the per capita ability of the native biota to resist invaders. Furthermore, modifications to selective environments are predicted not just to contribute to the establishment of non-indigenous species, but also to heighten the per capita impact of non-indigenous species on natives. The novel and sustained environmental changes that anthropogenic disturbances impose may often be enough to move a species out of the parameter space that defined its evolutionary history and to which it was adapted. A native species may therefore suddenly find itself in an environment that in key ways is just as novel as it is to a non-indigenous species. This leveling of the playing field may imply that native species are no longer guaranteed a prior-resident advantage in our globally disturbed biosphere.

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