Forum

Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions

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We present a framework for explaining variation in predator invasion success and predator impacts on native prey that integrates information about predator–prey naïveté, predator and prey behavioral responses to each other, consumptive and non-consumptive effects of predators on prey, and interacting effects of multiple species interactions. We begin with the 'naïve prey' hypothesis that posits that naïve, native prey that lack evolutionary history with non-native predators suffer heavy predation because they exhibit ineffective antipredator responses to novel predators. Not all naïve prey, however, show ineffective antipredator responses to novel predators. To explain variation in prey response to novel predators, we focus on the interaction between prey use of general versus specific cues and responses, and the functional similarity of non-native and native predators. Effective antipredator responses reduce predation rates (reduce consumptive effects of predators, CEs), but often also carry costs that result in non-consumptive effects (NCEs) of predators. We contrast expected CEs versus NCEs for non-native versus native predators, and discuss how differences in the relative magnitudes of CEs and NCEs might influence invasion dynamics. Going beyond the effects of naïve prey, we discuss how the 'naïve prey', 'enemy release' and 'evolution of increased competitive ability' (EICA) hypotheses are inter-related, and how the importance of all three might be mediated by prey and predator naïveté. These ideas hinge on the notion that non-native predators enjoy a 'novelty advantage' associated with the naïveté of native prey and top predators. However, non-native predators could instead suffer from a novelty disadvantage because they are also naïve to their new prey and potential predators. We hypothesize that patterns of community similarity and evolution might explain the variation in novelty advantage that can underlie variation in invasion outcomes. Finally, we discuss management implications of our framework, including suggestions for managing invasive predators, predator reintroductions and biological control.

Although invasions by predators often result in major impacts on native communities (Elton 1958, Dickman 1996, Williamson 1996, Mack et al. 2000, Gurevitch and Padilla 2004, Cox and Lima 2006, Salo et al. 2007), some non-native predators either fail to establish (Williamson 1996, Duncan et al. 2001, Simberloff and Gibbons 2004, Jeschke and Strayer 2005, Rao 2005), have relatively little impact if they establish (Bruno et al. 2005), or have positive effects on invaded communities (Rodriguez 2006). Understanding variation in the establishment success and impacts of different non-native predators on native communities is essential to developing a predictive understanding of the conditions that result in high-impact predator invasions. Analyses of invasion outcomes often split the invasion process into three stages: (1) arrival, (2) establishment/spread and (3) impact (Lodge 1993). Although differences in propagule pressure in the arrival stage can be important, we focus here on factors that influence how predator–prey interactions determine variation in outcomes in stages 2 and 3.

One hypothesis (the 'naïve prey' hypothesis) suggests that a lack of evolutionary history between non-native predators and the invaded community results in ineffective antipredator behavior by naïve prey that facilitates the establishment and increases the impacts of non-native predators (Diamond and Case 1986, Cox and Lima 2006, Freeman and Byers 2006). Naïve prey, however, do not always respond suboptimally to novel predators. A key issue is thus to develop a framework that identifies what aspects of prey or predator biology explain why naïve prey sometimes exhibit ineffective antipredator behaviors and thus suffer heavy predation, whereas in other cases, naïve prey respond effectively to novel predators.

Effective antipredator behaviors reduce direct predation (consumptive effects of predators, CEs), but often also result in non-consumptive effects (NCEs, e.g. energetically-costly alterations in prey behavior, morphology or life histories; Sih et al. 1985, Lima 1998, Peacor and Werner 2003, Creel and Christianson 2008). There is a growing recognition that these NCEs can have important population, community, and ecosystem level consequences (Peacor and Werner 2001, 2004, Werner and Peacor 2003, Preisser et al. 2005, Naddafi et al. 2007, Pangle et al. 2007, Schmitz et al. 2008, Creel and Christianson 2008). Indeed, a recent meta-analysis by Preisser et al. (2005) suggests that the fitness level consequences of non-consumptive effects (NCEs) can be equal to or stronger than consumptive effects (CEs). The NCEs of predators on prey may also 'spill over' and indirectly impact other members of the community leading to trait-mediated indirect interactions (Huang and Sih 1990, Abrams et al. 1996, Peacor and Werner 1997). For example, trophic cascades in aquatic systems appear to be largely driven by NCEs (Preisser et al. 2005). Despite their importance, the role of NCEs versus CEs in affecting invasions is poorly understood. A second key issue is thus to understand how non-native and native predators might differ in their consumptive and non-consumptive effects on prey, and how these differences might help to explain invasion outcomes.

Non-native predator invasion success, however, may be influenced not just by its evolutionary history and interactions with native prey, but also by the invader's interactions with new predators and competitors. Figure 1 shows the invasion of a non-native predator into a simple native ecosystem that includes a top predator capable of feeding on the invader, a native competitor, and several common prey taxa. As noted above, the 'naïve prey' hypothesis (link A in Fig. 1) suggests that a non-native predator's invasion and subsequent impact on native prey might be facilitated by a lack of effective antipredator behavior resulting from the evolutionary naïveté of the prey (Gamradt and Kats 1996, Coss 1999, Ricciardi and Atkinson 2004, Snyder and Evans 2006). The 'enemy release' hypothesis (link B) posits that the invasion of a non-native predator might be aided by a lack of top–down

control of the invader's population growth (Torchin et al. 2003, Colautti et al. 2004, Torchin and Mitchell 2004). Even a native community with its full complement of top predators might fail to exert top–down control and suppress a non-native intermediate predator if a lack of evolutionary history renders naïve, native top predators incapable of recognizing, capturing, or eating the introduced species. A related idea is the EICA hypothesis (evolution of increased competitive ability; Blossey and Notzhold 1995, Callaway and Ridenour 2004; link C). Invaders released from the predation pressure present in their native range can reduce their relative allocation to antipredator defenses and instead evolve increased competitive ability (Blossey and Notzhold 1995).

Although these hypotheses are inherently connected by overlapping trophic interactions, their interacting effects on invasion outcomes, and in particular, the possible role of naïveté in shaping these interactions needs further development. Moreover, given that non-native predators should also often be naïve to their new prey and new top predators, we might expect non-native predators to sometimes be ineffective predators on novel prey and poorly adapted to novel predators. When naïveté goes both ways, what gives non-native predators a 'novelty advantage' that facilitates their invasion success, as opposed to a novelty disadvantage that reduces invasion success?

Here, we develop a general hypothesis on the roles that evolutionary history, general types of prey responses to predators, and similarity of non-native predators to native predators play in explaining variation in the success and impacts of predator invasions. We discuss how non-native and native predators might differ in their consumptive, non-consumptive and total impacts on prey, and how these differences in CEs and NCEs might influence invasion outcomes. Broadening our framework to include multiple species interactions, we discuss inter-relationships between the naïve prey, enemy release and EICA hypotheses, and how they all might be influenced by prey and predator naïveté and behavior. Using this multi-species framework, we discuss how previous evolutionary history and ongoing evolution might predict conditions when non-native predators gain the novelty advantage required to successfully invade. Finally, we discuss management implications of our framework, including suggestions for enhancing management of invasive predators, predator reintroductions and biological control.

Naïve prey and predator invasions

We begin by considering the role of prey naïveté in predator invasions (link A in Fig. 1). Naïve prey that lack an evolutionary history with a non-native predator might often exhibit weak or nonexistent antipredator responses (Gamradt and Kats 1996, Freeman and Byers 2006, Smith et al. 2008). Prey naïveté may result in a failure to recognize predation threats, in inappropriate antipredator responses, or appropriate but ineffective responses (Banks and Dickman 2007). As a result, prey might suffer heavy predation (strong consumptive effects, CEs), but relatively little cost of antipredator response (weak non-consumptive effects, NCEs). In that case, non-native predators might have stronger CEs and weaker NCEs than native predators that share an evolutionary history with the native prey. This scenario assumes that native prey have
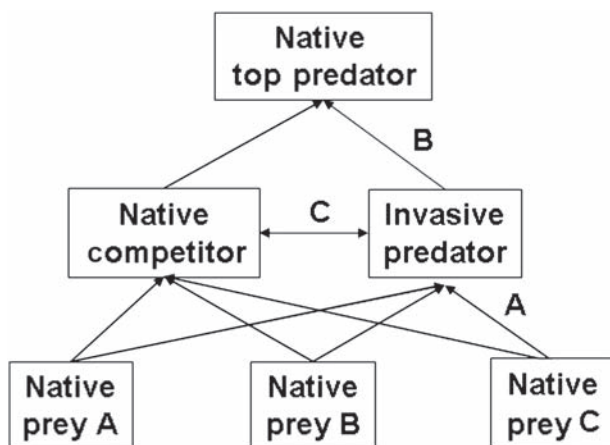

Figure 1. Three main hypotheses for how predator–prey interactions or competition might influence the success of a predator invasion. A = prey naïveté hypothesis; B = enemy release hypothesis; C = EICA (evolution of increased competitive ability).

evolved effective, plastic antipredator responses to native predators. Indeed, the usual operational definition of a NCE measures the cost of plastic antipredator responses (e.g. by comparing prey fitness in the experimentally-controlled presence vs absence of a predator; Preisser et al. 2005). An alternative possibility, however, is that prey might evolve fixed antipredator defenses (e.g. if predation pressure is predictably strong and the cost of plasticity is large). In that case, the magnitude of the CE generated by a non-native predator will depend on whether the fixed defense is effective or not. A large CE will emerge only if the fixed defense is ineffective. Regardless of its effectiveness, when defenses are non-plastic, alterations in the predator regime (including invasion of a non-native predator) should cause no NCE. Following the overall literature on NCEs versus CEs, our focus here is on plastic antipredator behaviors.

Many notable instances of introduced predators having major negative impacts on prey involve the effects of introduced predators on islands and ponds and lakes. Examples include the impact of brown tree snakes on birds (and other prey) on Guam (Savidge 1987), impacts of red foxes on small marsupials in Australia (Dickman 1996, Jones et al. 2004), negative consequences of trout introduction into alpine lakes for their amphibian and invertebrate prey (Knapp and Matthews 2000, Knapp 2005), and the impact of Nile perch, *Lates niloticus*, on haplochromine cichlids in Lake Victoria (Goldschmidt et al. 1993). Cox and Lima (2006) hypothesized that the stronger impacts of introduced predators on oceanic island communities (Diamond 1989, Case et al. 1992, Blackburn et al. 2004, Salo et al. 2007) and on freshwater systems (Moyle 1986, Vermeij 1991, Courtenay and Moyle 1992, Wilcove and Bean 1994) relative to terrestrial ones is due to the fact that prey are particularly predator-naïve in these regions. Although few studies on the impact of non-native predators on their prey provide information on prey behavior, the strong CEs associated with some high profile invasive predators appear to be caused by naïve prey exhibiting weak or inappropriate antipredator behaviors. This is analogous to the large impact of introduced herbivores in areas that previously had no herbivores. Here, plants may be evolutionary naïve and lack defenses against novel herbivory (e.g. domestic livestock), resulting in high impacts including extinction (Gurevitch and Padilla 2004).

Although it may often be true that non-native predators have large CEs on naïve prey, exceptions certainly exist. Non-native predators sometimes exert only weak or minimal effects on native prey, and even the impact of non-native predators with large overall CEs can vary widely among different prey species (Fagan and Hurd 1994, Grosholz et al. 2000, Knapp 2005). Recent reviews suggest that the relative impacts of predators on different prey species is more affected by variations in prey behavior rather than by the predator's diet selection (Sih and Christensen 2001). Prey that can hide or escape survive well, while those species that lack these options often suffer heavy predation. For non-native predators, this generality appears to also hold in the relatively few cases where information is available on variation in antipredator behavior (Knapp and Matthews 2000). In light of this fact, it becomes critical to understand why some naïve prey respond appropriately to a novel predator while other prey species do not.

One hypothesis concerning why an invading predator may have low impacts on a community is that prey response to a non-native predator varies depending on how similar the invader is to native predators. As noted above, strong impacts of non-native predators on prey appear particularly likely to occur in situations in which the native prey have historically lacked predators; e.g. on oceanic islands, or high altitude lakes (Moyle 1986, Diamond 1989, Vermeij 1991, Case et al. 1992, Wilcove and Bean 1994, Blackburn et al. 2004, Blumstein 2006). In these cases, it seems clear that the non-native predator is genuinely novel, in the sense of being completely outside the realm of experience to the prey. In situations where the native prey had evolved in concert with native predators, the impact of the invasive species might be a function of the similarity of non-native and native predators as perceived by prey. Even non-native predators might evoke appropriate antipredator responses in native prey species if the invader happens to be sufficiently similar to a pre-existing native predator, potentially inducing large NCEs on prey, and thus producing little overall change in the impact of predators on prey. A corollary to this idea is that the strongest CEs should be associated with truly novel predators.

If the degree of 'similarity' between native and non-native predators is important, how do we assess the similarity of an introduced and native predator? One possibility involves the degree of taxonomic similarity. A non-native fish is more likely to be recognized as dangerous if the invaded community already contains predatory fish. Although using taxonomic similarity is easily assessed, it may not always correlate with the degree of mechanistic or functional similarity existing between non-native-native predator pairs (Chalcraft and Resetarits 2003). We propose a more comprehensive, mechanistic approach to assessing predator similarity that follows the three stages of a generalized predator–prey interaction: encounter, detection/recognition, and response.

Encounter
In many systems, the rate at which a predator encounters a given prey species is primarily a function of the spatiotemporal overlap between the two species, as illustrated by the importance of predator and prey habitat use in determining the strength of NCEs (Preisser et al. 2007). In such cases, the similarity of non-native and native predators in the encounter phase can be measured by their spatiotemporal overlap in foraging activity or in their habitat domain (see Preisser et al. 2007 for an example that classifies habitat domain for 193 papers). If non-native predators are similar to native ones in their spatiotemporal pattern of activity, and native prey overlap little with native predators, then, assuming no substantial change in prey behavior, they should also have low overlap with the invader.

Detection/recognition
A low degree of spatiotemporal predator–prey overlap may also be due to active prey avoidance of predators (Lima 1998, Sih 1998), which requires prey to first detect and recognize danger. Understanding how prey assess predation risk requires knowledge of the sensory mechanisms responsible for the detection and recognition of predators. We propose a 'cue similarity' hypothesis that emphasizes the importance of two factors: 1) whether prey use general or specific cues to gauge risk; and 2) the degree of cue similarity between

non-native and native predators. Specific cues are emitted only by specific predators and thus are tightly associated with those predators. Thus, prey that rely on specific cues to gauge risk will exhibit an antipredator response only when they detect the specific predator. In contrast, general cues are produced by a relatively broad range of situations. Because general cues are not tightly associated with specific predators, prey that use general cues to identify risk will likely over-respond to many stimuli that are not actually risky.

Examples of prey use of general versus specific cues can be found in aquatic prey that respond to chemical cues associated with predation (Petranka et al. 1987, Chivers and Smith 1998, Kats and Dill 1998, Brown 2003). Chemicals from damaged conspecific or heterospecific prey constitute a very general cue capable of generating a prey response to any 'sloppy' predator. However, such general cues may overestimate predation risk if they are also produced by nonpredatory sources of damage. Similarly, some prey respond to fish chemical cues (Binckley and Resetarits 2003, Sih et al. 2003). Although these prey will respond to an invasive predatory fish, they are also likely to unnecessarily avoid non-predatory fish (Langerhans and DeWitt 2002). Other potential general cues include the presence of any novel organism (larger than a minimum threshold), or any large, moving object (Dill 1974, Sih 1986). Similarly, terrestrial rodents frequently respond to aspects of habitat structure that are indicators of risk from multiple predator types (Brown and Kotler 2004), and the general cue of habitat structure may be more informative than predator-specific cues (e.g. urines produced by specific predators; Orrock et al. 2004).

In contrast to such general cues, many other prey require either a more specific cue (Kotler et al. 1991, Jedrzejewski et al. 1993, Thorson et al. 1998), a mixture of multiple cues (e.g. simultaneous detection of chemical cues from specific predators and damaged prey (Sih 1986, Chivers et al. 2002, Schoeppner and Relyea 2005, Brodin et al. 2006)) or both chemical and visual cues from a specific predator (Luisa et al. 2004). An important component of such a prey response system should be whether prey respond to cue A or cue B, or respond only to cue A and cue B (Fig. 2d). Prey that use specific cues to gauge risk may fail to correctly assess the risk posed by an invasive predator. The degree of reliance upon specific chemical cues can vary both within and among species. In some species, different populations and different individuals within a single population respond differently to the same risk-related cues (Sih et al. 2003, Brodin et al. 2006).

Figure 2 illustrates three possible scenarios from a spectrum of possibilities for prey response to non-native predators. Non-native predators whose traits provide cues to native prey similar to those of native predators will likely be recognized as dangerous by native prey (Fig. 2a). If, however, the non-native predator's cues are quite different from native predators, then the ability of native prey to recognize the predator will depend on the generality of the cues used by prey to gauge risk. Prey that use specific cues (Fig. 2b) will tend to ignore the invader, exhibit little or no antipredator response (weak NCEs) and thus potentially suffer heavy predator induced mortality (strong CEs). In contrast, prey that rely upon general cues (Fig. 2c) will exhibit antipredator behaviors in response to a broader region of cue space and may still exhibit an antipredator response to even a truly novel invasive predator. Quantifying cue similarity between non-native and native predators, and the degree of variation in the type and precision of cues used by native prey should facilitate our ability to predict the impact of non-native predators.

The evolutionary history (i.e. both their phylogeny and history of selection pressures) of different prey species may also help explain why apparently similar prey species use different cues. Prey that use more general cues increase the probability that they will respond to a novel predator as well as the probability that they will respond unnecessarily to non-dangerous stimuli. Prey that rely upon more specific cues reduce the rate of unnecessary response while increasing their risk of not responding to a potential predator. The balance between these two competing selection pressures is likely determined by the degree to which some mistakes are more costly than others. If prey can easily escape attack by their native predators, the cost of using specific cues (and not responding to some predators until the last second) is relatively low. The benefit of using specific cues (and thereby reducing unnecessary antipredator behavior) should be particularly large if the costs of over-responding to risk are high (e.g. food is very scarce and only found outside of refuges). In contrast, prey that have difficulty escaping predators should favor more general cues because they
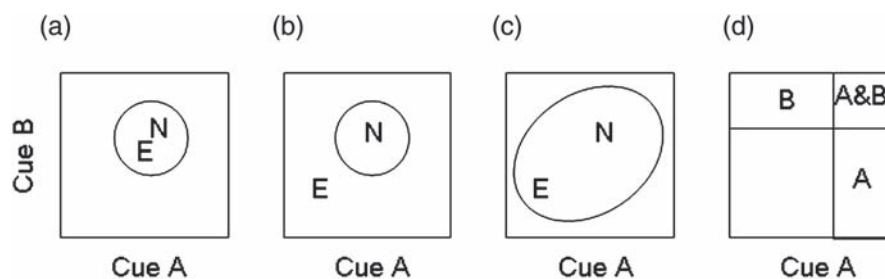

Figure 2. Cue use and prey recognition of non-native predators. Shown are two-dimensional cue spaces. N = cues produced by a native predator; E = cues produced by a non-native predator. The circle around each N is the cue space that elicits an antipredator response. (a) Native and non-native predators produce similar cues, and prey use specific cues. Prey recognize the non-native predator. (b) Native and non-native predators produce dissimilar cues, and prey use specific cues. Prey do not recognize the non-native predator. (c) Native and non-native predators produce dissimilar cues, but because prey use generalist cues, they recognize the non-native predator. (d) Prey recognition of a predator depends on how they use multiple cues. Prey could be alarmed by either A or B (above a threshold level for either), or might require cue A and B to be alarmed.

cannot afford to make the mistake of under-responding to predators. In a more general sense, quantitative information on the costs and benefits of using cues of different types and with different rates of spread and persistence should prove useful for explaining cue use and, in turn, predicting the response of naïve prey to new, non-native predators.

Response

Recognizing a non-native predator is necessary (but not sufficient) to ensure prey survival. To survive, prey must also respond appropriately to the non-native predator. Some studies have documented inappropriate prey escape responses to novel predators. For example, introduced New Zealand mudsnails in North America respond to crayfish (that were only recently introduced to New Zealand) by hiding under rocks or burrowing into the substrate. While this response is effective against predatory fish, it is an inappropriate response to crayfish that are often found under substrates. As a result, these snails suffer heavy predation by crayfish despite their behavioral response to crayfish chemical cues (J. Stapley, B. Ajie, A. Sih unpubl.). Another example of inappropriate prey response involves native water voles and introduced American mink in Europe (Macdonald and Harrington 2003). Here, native water voles have an innate fear of American mink and respond by taking refuge in burrows (suffering the non-consumptive costs of responding). However, this response is ineffective against female minks that are small enough to get inside the burrow, causing water voles to still suffer heavy predation.

As with detection/recognition, a key issue for understanding the impacts of invasive predators is whether prey use generalized or specialized antipredator responses (Lima 1992, Matsuda et al. 1994, Sih et al. 1998). Examples of specialized prey responses include predator specific microhabitat shifts or escape behaviors. Unfortunately for prey, responding to one predator can increase susceptibility to another species (Kotler et al. 1992, Warkentin 1995, Sih et al. 1998, Relyea 2003). For example, mayflies that flee bottom-foraging stonefly predators by entering the water column experience an increased chance of fish predation (Soluk and Collins 1988). Although prey might have evolved to adaptively balance the conflicting demands of responding to multiple native predators, it would not be surprising if prey often exhibit inappropriate specialized responses to a non-native predator. A generalized response might then be preferred even if it is less effective than a given specialized defense, if it is at least somewhat effective against most predators. For example, reduced prey activity (along with hiding in refuge) might generally reduce predator encounter rates. As a result, prey that rely on more generalized antipredator behaviors may be more likely to respond effectively to a novel predator.

Non-consumptive versus consumptive effects of invasive predators

Figure 3 shows a graphical representation of the overall effects (consumptive and nonconsumptive) of different predators on focal prey (see Creel and Christianson 2008 for a parallel framework). The total predator impact is the sum of consumptive and nonconsumptive effects (CE + NCE). The dashed line is the line of equal consumptive and non-consumptive

effects. Thin diagonal lines (of negative slope) are isoclines of equal total effect, with larger total effects represented by lines further from the origin. The heavy line represents CEs and NCEs associated with a range of possible levels of antipredator effort for a particular focal prey. The negative slope of the line reflects the assumption that there is a tradeoff: the greater antipredator effort that is required to reduce CEs results in larger NCEs (Lima 1998). Points on the upper left represent stronger antipredator effort resulting in weak CEs, but strong NCEs, whereas points on the lower right reflect weak antipredator effort resulting in strong CEs, but weak NCEs. Points below the line are unattainable. The 'concave up' shape of the curve reflects the assumption that prey that show adaptive antipredator responses can reduce predation rates (CEs) from high to intermediate with relatively little cost (small additional NCE), but that it is more difficult (more costly) to further reduce predation rates from intermediate to low levels.

When exposed to native predators, prey should exhibit adaptive antipredator responses that minimize total predator effects (point X). Here, we represented native predators as having roughly equal CEs and NCEs (see Preisser et al.'s (2005) meta-analysis for some examples). When prey encounter an introduced predator, they often exhibit weaker antipredator responses and thus suffer higher CEs, but lower NCEs. If the invader is similar to the native predator and prey exhibit an effective antipredator response, then the shift in relative importance of CEs and NCEs might be small (point Y1), whereas if the invader is truly novel, the shift might be to much stronger CEs and weak NCEs (point Z). Novel predators have both larger total effects on prey, and a much larger proportion of their total effect that comes through consumption per se. In the worst case scenario, non-native and native predators exhibit cue similarity, and thus prey respond, but prey responses to the non-native predator are ineffective. In that case, the nonnative predator
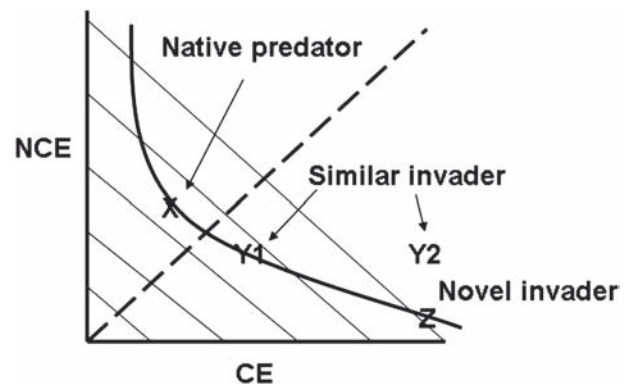

Figure 3. The relative impacts of consumptive effects (CEs) and non-consumptive effects (NCEs) of predators on prey. Native predators often have moderately strong CEs and NCEs (point X). If the non-native predator is similar to native predators, then the impact of the non-native predator might be similar to that of a native predator but with slightly higher CEs and slightly reduced NCEs (point Y1). Or, if prey respond to a similar non-native predator, but respond inappropriately, then the prey might still suffer high NCEs and elevated CEs relative to a native predator (point Y2). Finally, if prey do not recognize the novel predator, and thus do not respond strongly, they will likely suffer high CE, but with weak NCEs (point Z).

should cause large CEs and large NCEs (point Y2 in Fig. 3). Over time, if prey survive an initial period of heavy predation, prey should shift towards more adaptive antipredator behavior that will likely move them towards point X. This could be over evolutionary time (Losos et al. 2006, Strauss et al. 2006) or via learning within a generation (Berger et al. 2001, Caro 2005).

If total effects are not altered much, does the fact that invasive predators tend to produce stronger consumptive and weaker non-consumptive effects have important consequences for predator–prey dynamics? Several lines of reasoning suggest that the answer might often be yes. First, a given predator's NCEs can spread over a much larger spatial scale than that predator's CEs. Direct CEs of predators can only occur in the predator's immediate neighborhood. In contrast, whenever predator cues travel long distances, predators can scare prey that are far from the predator (Sih et al. 1992). In addition, predator-induced prey dispersal (a NCE) can produce strong indirect predator effects far from the predator itself, and these effects can extend to metapopulation and metacommunity dynamics (Orrock et al. 2008). For example, carnivores often have major effects on plants by driving herbivores out of local patches and thus freeing plants from herbivory in the patches with carnivores. This can have the additional effect of causing large increases in herbivory in the herbivores' destination sites (Power et al. 1985). Predators then have strong 'remote control' effects on communities in distant sites where the predators never go (Orrock et al. unpubl.). When naïveté makes prey NCEs negligible, invasive predators are less likely than native predators to have strong remote control effects.

NCEs also often occur on different time scales (thus generating different time lags) than CEs. NCEs associated with dispersal are faster than CEs; prey dispersal can reduce prey density much faster than predation per se, and prey can recover much more quickly via recolonization than via reproduction. In contrast, NCEs involving reduced feeding rates that eventually translate into reduced growth and fecundity, or future starvation might be much slower than predation per se. Longer time lags tend to destabilize population dynamics (Luttbeg and Schmitz 2000). Thus any shift in relative importance in NCEs versus CEs associated with a predator invasion could have important affects on population stability.

In addition, NCEs can generate counter-intuitive outcomes that do not occur from CEs per se. For example, in streams, prey often strongly reduce their activity when predators are present, resulting in reduced prey dispersal from the patch. If prey continue to drift into the patch, the counter-intuitive result is a build-up of prey in areas with more predators (Sih and Wooster 1994, Wooster and Sih 1995). Novel invasive predators are less likely to induce this counter-intuitive effect.

Most importantly, NCEs decouple the trophic link between predators and prey. If prey exhibit strong, effective antipredator behaviors that result in low CEs, predators can have strong NCEs on prey, but still not gain the energy required to fuel rapid predator population growth. In contrast, if prey show little antipredator response to invasive predators, and get eaten instead, this yields strong, trophic benefits for the invasive predators. This, in turn, should help

non-native predators to establish more easily, outcompete native predators (that have weaker absolute CEs on prey), and attain higher maximum densities.

Note that most standard ecological theory ignores NCEs (but see Abrams 1995, Bolker et al. 2003, Preisser and Bolnick 2008). For example, in standard Lotka–Volterra type models, species interactions typically involve CEs and not NCEs (Peckarsky et al. 2008). Given that NCEs are often very important in native communities (Preisser et al. 2005), while CEs might generally be more important in interactions involving non-native predators, paradoxically, standard theory might better fit predator invasions than native communities. Simple Lotka–Volterra predator–prey models (with a time lag) show that if predator attack rates are high (as they might be with novel predators and naïve prey), the outcome can be a rapid increase in predator numbers to well above the predator's carrying capacity, resulting in overconsumption of prey, driving a crash in prey numbers, followed by either a crash in predator numbers (Simberloff and Gibbons 2004), or if predators can disperse, predator invasion into new areas with naïve prey. This 'boom-bust' pattern has indeed been observed in several predator invasions (e.g. least weasel, Chinese mitten crab) although the mechanisms underlying crashes in predator densities are not entirely clear (King 1990, Korpimäki et al. 1991, Rudnick et al. 2003).

Naïve prey, naïve top predators and enemy release

Up to this point, we have emphasized the role of prey naïveté in facilitating predator invasions. The success of predator invasions depends also, however, on their interactions with their own predators (native top predators) and competitors. The enemy release hypothesis posits that the success of invasive predators is aided by a lack of predation (or parasitism) on the invaders. This release could occur either because the invaded community simply lacks relevant top predators, or because the resident top predators (due perhaps to naïveté) are ineffective in consuming the invaders. EICA is the corollary idea that enemy release allows invaders to reduce their antipredator effort and thus (assuming a tradeoff between antipredator and competitive abilities) increase their competitive ability. Both hypotheses have received mixed support (Agrawal and Kotanen 2003, Colautti et al. 2004, Mitchell et al. 2006); however, most tests have involved invasive plants and their enemies, and not invasive predators.

CEs and NCEs play an important role in these hypotheses. The enemy release hypothesis focuses on the invader's release from the CEs of top predators, while the EICA hypothesis focuses on one main aspect of release from the NCEs of top predators. While the EICA idea is couched in terms of evolutionary release, it could also represent a behavioral release (i.e. reduced antipredator behavior and thus increased foraging activity). In the present context, it would be insightful to elucidate factors that influence the relative magnitude of CE and NCE release, and their relative importance in facilitating predator invasions.

Interestingly, the main predictions of the enemy release and EICA hypotheses can also be explained, in part, by the effects of prey naïveté on the foraging success of non-native predators. An invasive predator seems most likely to be released from predation by top predators in the invaded

community if the invader does not resemble other predators (competitors) in the invaded range. With this enemy release, it can then evolve increased competitive ability and ultimately outcompete native predators. Moreover, if an invasive predator is dissimilar to native predators, it will likely also not be recognized as dangerous by native prey. The weak antipredator response of naïve native prey (relative to their response to native predators) should allow the invader to enjoy high feeding and growth rates that contribute to outcompeting native predators. That is, truly novel invasive predators might outcompete native predators because they have the double advantage of naïve top predators and naïve prey.

Similarly, a weak effect of a top predator on introduced intermediate predators (i.e. enemy release of the introduced predator) might be enhanced by prey naïveté about the introduced predator. If prey naïveté contributes to high energy intake rates by invasive predators, this should result in invaders that are vigorous (ready to escape attacks), and in good condition, and thus ready to hide more readily despite the energetic cost of hiding.

In contrast, if the non-native predator is fundamentally similar to a native predator, this could increase competition between non-native and native predators and make it more difficult for the invader to establish. This idea has been termed Darwin's naturalization hypothesis (Darwin 1859, Daehler 2001, Wu et al. 2004, Ricciardi and Mottiar 2006). High similarity of an invader to a native predator, however, can also reduce invasion success via reduced prey naïveté. If prey are exposed to a new predator that resembles a native predator, they will likely recognize it as dangerous and avoid it effectively. This will reduce the invader's feeding rate and thus its ability to establish and increase in abundance, not due to competition per se, but due to lack of prey naïveté.

Community similarity, evolution and novelty advantages that facilitate successful invasions

When a novel, non-native predator invades a new community, all species interactions are new. Prey and top predators are naïve about the introduced predator, and conversely, the introduced predator is naïve about its new prey and predators. Above, we emphasized the hypothesis that the naïveté of prey and top predators might give non-native predators a 'novelty advantage' that facilitates their successful invasion. Note, however, that it is also conceivable that introduced predators might suffer a 'novelty disadvantage' because they are naïve about the new prey and top predators in the invaded community. Introduced predators might then exhibit inappropriate behaviors that tend to result in poor foraging success on native prey or poor ability to cope with native top predators, likely increasing the ability of the invaded community to resist invasion. The general notion that invasion success might be limited by increased enemy pressure in the invaded range has been termed the 'increased susceptibility hypothesis' (Colautti et al. 2004, Bruno et al. 2005). The additional insight here is that enemy-based resistance to invasion might be due not only to an increased number of potential enemies in the invaded range, but also to the invader's naïveté resulting in poor responses of invaders to native top predators. The notion that the invader's naïveté about the invaded community is important is a special case

of the general idea that invasion success depends on traits of the potential invader and how those traits might allow the invader to cope with challenges in the invaded community (Lodge 1993, Duncan et al. 2001, Marchetti et al. 2004, Rehage et al. 2005).

Given that in principle, naïveté could either facilitate or prevent invasions (introduced predators could either enjoy a novelty advantage or suffer a novelty disadvantage), why do we so often see non-native predators with apparent novelty advantages that allow them to become high impact, invasive pests? One possibility is that novelty advantages are actually not common. High impact, invasive predators might simply represent the relatively rare instances of where an invader does enjoy a novelty advantage over native prey and predators. Recall that three invasion outcomes appear to be common. (1) very often, invading predators simply fail to establish (Mack et al. 2000, but see Jeschke and Strayer 2005). (2) sometimes, they establish and immediately become abundant pests, and (3) sometimes they establish but remain at low numbers for a long period before later, suddenly become abundant pests. A hypothesis for explaining these three outcomes is that outcome (1) is associated with invading predators that happen to come in with a novelty disadvantage, outcome (2) is where they come in with a novelty advantage, and outcome (3) arises when they come in 'novelty neutral' (where they are just 'pre-adapted' well enough to persist, but not to grow in numbers) but later evolve traits that allow them to increase to high numbers. In this context, a key question is: can we predict in advance when an invader might arrive with a novelty advantage? We hypothesize that a non-native predator will be most likely to enjoy an immediate novelty advantage if that predator's own native, source community is functionally similar to the invaded community except that the invaded community lacks a species similar to the invader. In that case, the invading predator should have an evolutionary history that allows it to respond effectively to the invaded community's prey, predators and competitors, but the invaded community's prey, predators and competitors will be functionally naïve (and might thus respond poorly) to the new, non-native predator.

To explain outcome (3) where a long time lag elapses before non-native predators become highly successful, we follow Facon et al. (2006) in using an eco-evolutionary approach. Our hypothesis focuses, in particular, on the possible importance of the fact that invaders are initially rare. 1) an initially rare invading population likely has low genetic variation; and 2) an initially rare species might enjoy a 'rare invader' selective benefit, where the invader is under strong selection to adapt to the invaded community while members of the invaded community experience only weak selection to adapt to the invader. Initial low genetic variation might play a role in explaining the poor establishment success of many invaders although population bottlenecks do not necessarily preclude rapid adaptation (Sax et al. 2007). To attain pest status, however, the invader must evolve to become better adapted to the invaded community (Kinnison 2008). Increased adaptation might come about through repeated invasions (bringing in new genetic variation), and the hypothesized rare invader selective benefit that allows invaders to evolve adaptations faster than the members of the invaded community (Kolbe et al. 2004). After what might be a substantial latency period, when the degree of invader

adaptation passes a threshold, the invader then explodes to pest levels. Invasions are known to induce evolution in both the invader (Grosholz and Ruiz 2003) and members of the invaded community (Strauss et al. 2006). The suggestion here is to identify and test predictions on conditions that allow the invader to evolve faster than its invaded community.

Management implications

A major goal of the study of invasion ecology is to predict situations where non-native predators are likely to have large, adverse impacts on the invaded community. Predicting vulnerable conditions alerts managers to situations where action may be required before non-native predators actually reach an area. Thus, the application of prey behavior and general behavioral principles to conservation problems needs to become a priority (Blumstein and Fernandez-Juricic 2004). We predict that invasive predators will have particularly large impacts on communities where prey are naïve in the sense that their evolutionary history either includes no strong predation pressure, or no exposure to predators that are fundamentally similar to the invader. Taxonomic similarity might often be a reasonable indicator of functional similarity; however, more mechanistic metrics that can, in theory, be quantified include cue similarity and foraging mode similarity. Prey naïveté should also influence the invader's ability to cope with top predators (enemy release) and competition.

If prey lack an evolutionary history with predators that are similar to a non-native predator, we predict that prey will show weak antipredator responses to the non-native predator, and might thus suffer heavy predation (CEs). In contrast, prey that share an evolutionary history with predators that are similar to the non-native predator might respond appropriately, resulting in high NCEs. While high NCEs can represent an important effect of an invasive predator (Pangle et al. 2007), even stronger long-term impacts may occur with CEs (as compared to NCEs) because CEs can fuel a large increase in predator density. In the worst case scenario, where prey have an evolutionary history of predation, but only from predators that do not resemble the new invader, prey might respond strongly, but inappropriately, and thus suffer high CEs and high NCEs. The corollary, that a new predator may be more problematic if there are prey in its native range that are similar to prey in the habitat it is invading, also applies.

If prey naïveté contributes to predator invasion success and negative impacts on prey, a potential management strategy might be to help native prey learn or evolve to better respond to the novel predator. If prey can learn antipredator behavior (Griffin et al. 2000, Blumstein and Daniel 2002), managers can train prey to be less naïve by providing them with simulated predatory experiences. Alternatively, managers can seed the area in front of a predator invasion front with prey that are not naïve; i.e. they can translocate prey from areas with an evolutionary history with the 'non-native' predator into areas that will likely soon be colonized by the non-native predator (Schlaepfer et al. 2005). This strategy seems most likely to be effective in prey with substantial social learning of antipredator behavior (Caro 2005). This suggestion is obviously related to the reintroduction policy of providing prey with anti-predator training to reduce the negative impact of predation on the success of reintroductions (McCallum et al. 1995, Griffin et al. 2000). Of course, translocations can have evolutionary and ecological problems, so this method must be approached with caution.

Conversely, managers might attempt to inhibit the non-native predator from adapting to their new environment. Efforts to cull predators could be directed at the individual predators that have become best adapted to their new environments. By baiting traps with cues from native prey, placing the traps in habitats preferred by native prey, or capturing predators that are matching the temporal patterns of native prey, managers may be able to retard predator adaptation and improve the chances of prey in the race to adapt well to the new predator–prey interaction.

Other potential behavioral, cue-based strategies for limiting invasion success are based on the enemy release and EICA hypotheses. If part of the success of a non-native intermediate predator involves enemy release derived from the naïveté of top predators relative to the invader, then managers might attempt to teach top predators to attack the invader. Or, if the non-native predator's ability to outcompete native predators derives from EICA associated with the non-native predator's release from having to respond to predation risk, managers might reduce these effects by introducing cues from the invader's natural predators (as opposed to the natural predator itself).

Another set of issues involves unexpected negative impacts of intentional introductions of predators – of glamour species (e.g. wolves), or species with an ecosystem function-including biological control agents. Introductions of large, glamorous predators often involve reintroducing predators into areas that they occupied in the recent past. Whether prey are naïve or not depends on the rate of prey loss of antipredator behavior during the period when these predators have been missing. In some cases, prey have apparently retained their antipredator behavior for hundreds or even thousands of years after predator local extinction (Byers 1997, Coss 1999, Blumstein and Daniel 2002, Blumstein 2006). In other cases, prey appear to have lost their antipredator behavior within a few generations, but retain the ability to re-learn antipredator behavior quickly (Berger et al. 2001, Berger 2007). A better understanding of variation in prey retention of antipredator behavior should prove valuable.

In contrast, predator introductions for biological control of pests often involve bringing the invader into a community where the target taxon has coevolved with the invader, but where the rest of the community is naïve to the invader. Often, these biological control agents are chosen to be specialists that are unlikely to feed on non-target taxa; however, depending on cue similarity between these introduced predators and native predators, they might still induce some NCEs in non-target taxa. Non-native generalist predators have also been used for biological control despite their potential negative impacts on non-target species. A best case scenario is where the generalist drives the pest to low levels, but then rather than crash, it maintains itself at moderate densities by feeding on non-target taxa. The generalist is then ready to switch back to the pest if the pest threatens to become abundant. The fact that often only the target species shares an evolutionary history with the biological control agent,

however, suggests an alternative worst case scenario where the target pest species (which has an evolutionary history with the introduced predator) responds well to the biological control agent, whereas naïve, non-target taxa respond poorly and suffer heavy predation.

A possible example of this latter scenario involves the introduction of foxes into Australia to control rabbits. Since rabbits had an evolutionary history with fox, they apparently responded appropriately, and did not suffer heavy predation. In contrast, several marsupials that lacked an evolutionary history with a fox-like predator did not apparently exhibit adaptive antipredator behaviors and were instead decimated (Dickman 1996). Clearly, a better understanding of predator–prey naïveté, similarity of native and non-native predators, and prey cue use and escape responses should help us to avoid these worst case scenarios.

Future directions

Given the importance of anti-predator behavior for affecting the dynamics of individuals, populations, and communities and the significant effects that introduced predators can have on introduced communities, future work should endeavor to understand the role of anti-predator behavior in affecting biological invasions. Although not exhaustive, we suggest five areas where future studies would be informative.

(1) To better understand variation in the ability of naïve prey to cope with non-native predators, we suggest a more thorough integration of invasion ecology with sensory/cognitive ecology and behavioral ecology of both predators and prey. In particular, it should be useful to compare prey populations or species to see if differences in cue use explain differences in antipredator responses that underlie relative abilities to cope with native predators, functionally similar non-native predators, and functionally novel non-native predators.

(2) To better understand the role of consumptive versus nonconsumptive effects in predator invasions, we need more experiments designed to quantify the relative importance of CEs versus NCEs for non-native versus native predators; contrasting, in particular, CE and NCEs for non-native predators that are functionally similar versus different from native predators.

(3) To better understand the roles of prey and predator naïveté in a multi-species context, we need to examine interactions between the naïve prey, enemy release and EICA hypotheses. For example, in an invaded community, how might prey naïveté affect not just feeding rates of non-native predators on native prey, but also behavioral responses and the ability of non-native predators to cope with native top predators? These interactions may be particularly important to understand in modern landscapes, as anthropogenic habitat alteration often leads to the local extinction of keystone predators and the proliferation of smaller carnivores (i.e. mesopredator release; Crooks and Soulé 1999), which may subsequently alter opportunities for invasive predators to become established.

(4) To better understand variation in initial novelty advantages (vs disadvantages) enjoyed by non-native predators,

a first step could be to use literature surveys to test our suggested hypothesis on how community similarity might explain the outcomes of previous invasions.

(5) Finally, new models on the coevolution of non-native predators and native species should be useful for generating more precise, general predictions on how propagule pressure, genetic variation and selection pressures on non-native versus native species might determine the evolution of species interactions that influence long-term invasion outcomes.

Insights generated from the above should then yield useful ideas for guiding various management issues associated with non-native predators including advance warning on non-native predators that are particularly likely to have strong negative impacts on prey, and possible manipulations of the naïveté of native predators or prey.

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