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MORE HARM THAN GOOD: WHEN INVADER VULNERABILITY TO PREDATORS ENHANCES IMPACT ON NATIVE SPECIES

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Abstract. Invasion biologists typically regard susceptibility of an invasive species to native predators as a fortuitous condition that increases biotic resistance to the invasion. The line of reasoning is that predation weakens the net impact of the invader and reduces its ability to displace native competitors. However, predation on invasives is a coupled interaction; every invader consumed also enhances the predator population. If these predators also consume native species, then the invader's indirect effect via predators (i.e., apparent competition) could be more harmful to natives than the effect of resource competition from the exotic. We apply general community ecology theory to determine the conditions under which the net effect of predation on the exotic species is to extirpate the native competitor. An approximation to these conditions provides a simple metric to estimate the threat of native species extinction due to apparent competition posed by an invader.

Key words: *apparent competition; biocontrol agent; biological control; biological invasions; biological resistance; competitive exclusion; exotic species; exploitative competition; nonindigenous species.*

INTRODUCTION

A native predator that attacks an introduced species is typically viewed as a strong component of biotic resistance to invasion (Elton 1958, Levine et al. 2004). Predation reduces the invader's population growth rate and density, and thereby alleviates the invader's competitive impact on native analogues (Robinson and Wellborn 1988, Baltz and Moyle 1993, Trowbridge 1995, Byers 2002). However, when a native predator consumes an exotic species, losses to the invader population are converted to additional predator biomass. Hence, predation on an exotic species can indirectly harm the predator's native prey (Roemer et al. 2001, Rand and Louda 2004). Which process is more detrimental for a native consumer—resource competition from a nonindigenous species or increased losses to a native predator population that is subsidized by the invader (Fig. 1)?

Community ecologists have recognized the general importance of negative indirect effects between species mediated through a shared predator, or apparent competition (Holt 1977). This concept is at least implicitly recognized by most biological control practitioners

when intentionally introducing exotic species (e.g., Wajnberg et al. 2001). Screening potential biocontrol agents for prey specificity is an ethically mandated, established procedure that, while minimizing the direct impact on nontarget species, also minimizes the risk of apparent competition on native prey species at the same trophic level. However, the possibility of apparent competition has until recently been largely ignored by invasion biologists (but see Courchamp et al. 2000, Byers 2005). This neglect presumably stems from a simple lack of appreciation for the strength of indirect interactions, and also from the absence of a clear rule of thumb regarding the net effect of predation on an exotic species: invasion biologists and resource managers must assess multiple direct and indirect interactions with positive and negative effects when making decisions about control measures.

General theoretical treatments of direct and apparent competition have focused on their consequences for community structure and dynamics (Grover and Holt 1998, Chesson 2000, Chase et al. 2002). This body of theory attempts to predict the characteristics of competitors that permit coexistence, and the characteristics and abundances of species that are expected to coexist along a gradient of productivity or predation intensity (e.g., Holt 1977, Abrams 1993, Holt et al. 1994, Leibold 1996, Grover and Holt 1998). One generalization

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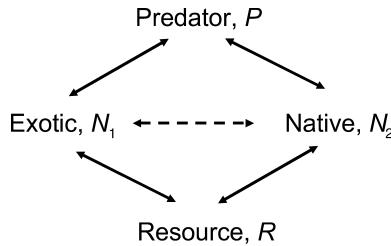


FIG. 1. When native and exotic consumers share a predator, predation on the exotic species can have a negative indirect effect on the native (dashed arrow). Predation on the exotic species is an important component of biotic resistance to the invader, but also can intensify the impact of the predator on the native prey. The net effect of the exotic on the native consumer depends on the relative contributions of resource competition and enhanced predator population growth rate (i.e., apparent competition).

that has emerged from these analyses is that if relative attack rates on each consumer are held constant, the more vulnerable competitor decreases with increasing predator efficiency. However, increasing the attack rate on only one consumer can, for some parameter values, depress the abundance of the other consumer (Holt 1977, Abrams 2004). The latter result is particularly relevant to biological invasions. If a native predator consumes an exotic prey species, under what conditions is the effect of apparent competition likely to outweigh the direct effect of predation on the exotic and drive the native competitor extinct?

We demonstrate the application of general community ecology theory to this question using a simple food web model. We employ a minimal representation of the food web to highlight the technique and our definition of risk. The model contains two key features. First, we explicitly model the feedback from prey to predators, such that increasing predation intensity on the invader raises the predator population growth rate. Second, predator preference for the exotic relative to the native prey is our measure of predation intensity on the exotic. We define risk as the proportion of values of predator preference for the exotic for which the native consumer is driven to extinction. With this approach, general analytic results can be obtained for the case in which native and exotic consumers interact via both direct and apparent competition. We then use an approximation to derive a simple metric to assess the likelihood of native extinction due to apparent competition. Although the metric is an approximation derived from a simple model, the general results have heuristic value for predicting the effects of exotic species that are susceptible to native predators.

MODEL AND RESULTS

The invasion scenario in which an exotic consumer competes for the same resource and shares a predator with a native consumer generates a food web (Fig. 1) that is identical to the structure that community ecol-

ogists use to study predator-mediated coexistence of competitors (e.g., Armstrong 1979, Leibold 1989, Holt et al. 1994). The most appropriate form of the model depends on the details of a given system, such as particular resource growth functions and consumer functional responses. We employ the simplest representation of four species at three trophic levels that contains sufficient detail to model direct and apparent competition between native and exotic consumers. We apply standard equilibrium coexistence analysis to determine species and environmental characteristics for which predation on the exotic poses a high risk to the native consumer.

We assume logistic growth for the resource (R) and linear functional responses for both competitors (native N_1 , exotic N_2) and the predator (P). Hence the population dynamics obey the following equations:

$$\begin{aligned} \frac{dR}{dt} &= \left[r \left(1 - \frac{R}{K} \right) - (a_1 N_1 + a_2 N_2) \right] R \\ \frac{dN_1}{dt} &= (\varepsilon_1 a_1 R - m_1 - b_1 P) N_1 \\ \frac{dN_2}{dt} &= (\varepsilon_2 a_2 R - m_2 - b_2 P) N_2 \\ \frac{dP}{dt} &= (e_1 b_1 N_1 + e_2 b_2 N_2 - d) P. \end{aligned} \quad (1)$$

The resource has intrinsic rate of increase r and carrying capacity K . Competitor i consumes the resource with attack rate a_i and conversion efficiency ε_i , and suffers density independent mortality at rate m_i . Similarly, the predator attack rate on competitor i is b_i , and the conversion efficiency is e_i . In the absence of prey, the predator population decreases with death rate d .

If the propagule of a nonindigenous species arrives in the system with the three native species (resource, consumer, and predator) at equilibrium, three outcomes are possible: (1) the invader population grows and the system reaches a new equilibrium with all four species at positive densities; (2) the invader population grows and the native competitor (and under some conditions the predator also) declines to extinction; (3) the invader population cannot grow. We interpret these three outcomes in terms of general competition theory. An important feature of the model in Eq. 1 is that coexistence conditions for the two consumers are mathematically identical to conditions for each consumer successfully invading the three-species food chain when that consumer is initially absent (see Appendix). Hence, Outcome 1 corresponds to predator-mediated coexistence of N_1 and N_2 . Outcomes 2 and 3 correspond to competitive exclusion of N_1 and N_2 , respectively. Coexistence of the two competitors in the absence of predators is not possible in this model (Armstrong and McGehee 1980; the coexistence condition that is derived from Lotka–Volterra competition models [i.e., that intraspe-

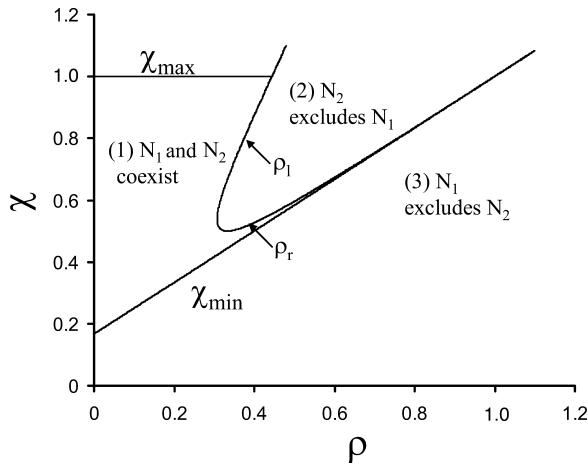


FIG. 2. Coexistence boundaries for native (N_1) and exotic (N_2) competitors in the food web depicted in Fig. 1. The relative resource consumption rate of the exotic ($\chi = a_2/a_1$) must satisfy $\chi_{\min} < \chi < \chi_{\max}$ (Region 1) for predator-mediated coexistence of N_1 and N_2 . Coexistence is further constrained by the possibility that apparent competition excludes the native consumer (Region 2). For $\chi < \chi_{\min}$, invasion of N_2 is not possible (Region 3). For a given value of χ , Region 2 is bounded by left and right values of preference, ρ_l and ρ_r , (exact solutions to Appendix Eq. A.7 for ρ_l and ρ_r , which meet at the minimum of the boundary). Parameters: $\varepsilon_1 = \varepsilon_2 = 1$, $e_1 = e_2 = 1$, $m_1 = m_2 = 0.01$, $a_1 = 0.1$, $b_1 = 0.1$, $r = 0.05$, $K = 1$, $d = 0.02$. Risk $\omega = 0.6$. (See *Model and Results* for definitions of parameters.)

cific competition outweighs interspecific competition] cannot be satisfied when only a single resource is available).

Our goal is to determine how the possibility of native extinction varies with predator preference for the exotic species. We quantify preference as the proportion of each prey type in the predator’s diet relative to the proportion of that prey type in the environment. For the model in Eq. 1, this quantity is consistent with Johnson’s (1980) definition of resource preference. In general, the appropriate measure of preference depends on the predator’s functional response; for a type 1 functional response, preference is equal to the ratio of attack rates (i.e., b_2/b_1 in Eq. 1 [Chesson 1978, 1983]).

The general technique to find the boundaries in parameter space that distinguish coexistence from competitive exclusion has been described elsewhere (e.g., Armstrong 1979), and we have placed the mathematical details in the Appendix. We present the coexistence conditions in terms of two parameter combinations, predator preference for the exotic, $\rho = b_2/b_1$, and the resource consumption rate of the exotic relative to the native, $\chi = a_2/a_1$ (Fig. 2). The parameters ρ and χ express the strengths of the two pathways through which the exotic competitor can affect the native consumer—boosting a shared predator (ρ) or consuming a shared resource faster (χ). In general, predator-mediated coexistence is possible only if the species that is the weaker resource competitor is also less susceptible

to predation (e.g., $\chi < 1$, $\rho < 1$, and all other parameters equal for N_1 and N_2). Hence, for a given predator preference for the exotic (ρ), coexistence requires that the exotic possess sufficient competitive strength to invade ($\chi > \chi_{\min}$), but not be so strong as to extirpate the native in the absence of predators ($\chi < \chi_{\max}$). The competitive strength of the exotic species must increase with increasing predation in order to invade; hence, χ_{\min} increases with ρ . However, χ_{\max} depends only on the relative competitive strengths of the two consumers, and is independent of ρ . For sufficiently high preference, there is a point at which $\chi_{\min} = \chi_{\max}$; to the right of this point an exotic with $\chi < \chi_{\min}$ cannot invade, whereas an exotic with $\chi > \chi_{\min}$ extirpates the native (Fig. 2).

Between χ_{\min} and χ_{\max} coexistence is possible (Fig. 2, Region 1), but not certain. A third condition specifies a region in which the exotic augments the predator population and apparent competition excludes the native competitor (Fig. 2, Region 2). This region occurs for intermediate values of predator preference for the exotic. For lower values of ρ , consumption of the exotic does not increase predator productivity enough to make apparent competition outweigh the superiority of the native in resource competition. For higher values of ρ , the direct effect of predation on the exotic is greater than the effect of apparent competition on the native consumer. Increasing ρ past the boundary of Region 2 moves the system into an extremely narrow region in which coexistence is again possible (Fig. 2, Region 1), then into a region in which the exotic is extirpated by predation (Fig. 2, Region 3).

We now reformulate our original question more specifically in terms of the theoretical framework summarized in Fig. 2. If an exotic species with relative competitive strength χ arrives and the predator does not attack this novel prey, then $\rho = 0$ and the system lies on the χ -axis. However, if the predator does attack the invader ($\rho > 0$), what is the risk that the addition of apparent competition will extirpate the native? The value of predator preference must lie to the left of the boundary separating Regions 1 and 2 from Region 3 (i.e., to the left of χ_{\min}), otherwise the exotic would be unable to invade. Therefore, for a successful invader with a given value of χ , the risk of extirpation of the native species by apparent competition is proportional to the width of Region 2 relative to the total width of Region 1 and Region 2 (i.e., the horizontal distance between the χ -axis and χ_{\min}). Note that for small χ Region 2 does not exist and the risk of native species extinction is zero.

We present analytic results for the width of Region 2 in the Appendix. In general, the boundary of Region 2 can be expressed as left and right bounds of ρ for a given value of χ , or upper and lower bounds of χ for a given value of ρ . The end result is identical: to emphasize the risk posed by predation, we take the former approach to find the width of Regions 1 and 2. Given the curvilinear boundaries (Fig. 2), it is not surprising

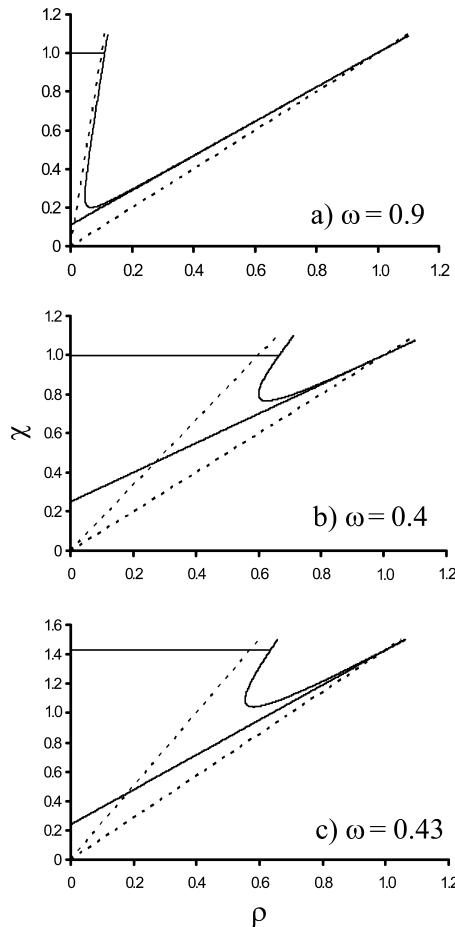


FIG. 3. Altering parameter values (curves are as labeled in Fig. 2) changes the risk of native species extinction via apparent competition, ω . (a) Increasing productivity ($r = 0.2$) increases the width of Region 2 relative to Region 1, and therefore increases ω . (b) Increasing predator death rate ($d = 0.03$) decreases the width of Region 2. (c) Decreasing exotic conversion efficiency ($\varepsilon_2 = 0.7$) reduces the width of Region 2 and increases the range of relative consumption rates (χ) in which the native consumer can persist in the presence of the exotic. Dotted lines indicate the approximations (Eqs. 2–4) to the exact boundaries. These approximations are increasingly accurate for high-risk scenarios.

that the expression for the width of Region 2 is cumbersome. To obtain greater insight into the qualitative effects of each parameter on the risk of apparent competition, we derive a simple linear approximation to the analytic solution for the boundaries of Region 2 (see Appendix; Fig. 3). The approximation rests on the assumption that each competitor's per capita growth rate is high when predators are absent and the resource is abundant (i.e., when $R = K$, $\varepsilon_i a_i R = \varepsilon_i a_i K$ is large relative to m_i). With this assumption, $\varepsilon_i a_i K - m_i \approx \varepsilon_i a_i K$, or $m_1 \approx 0$ and $m_2 \approx 0$. The result is the following pair of expressions, which approximate the left and right boundaries, respectively, of Region 2:

$$\rho_l \approx \frac{a_1 d}{e_2 b_1 r} \chi \quad (2)$$

and

$$\rho_r \approx \frac{\varepsilon_2}{\varepsilon_1} \chi. \quad (3)$$

With the same approximation ($\varepsilon_i a_i K - m_i \approx \varepsilon_i a_i K$), the right boundary of Region 1 is identical to Eq. 3 (see Appendix). The risk of native extinction due to apparent competition from a successful invader, which we denote ω , is therefore

$$\omega \approx \frac{\rho_r - \rho_l}{\rho_r} = 1 - \frac{a_1 d \varepsilon_1}{e_2 b_1 r \varepsilon_2}. \quad (4)$$

In summary, for a given value of χ , the risk to the native competitor from apparent competition is equal to the width of Region 2 relative to the sum of Regions 1 and 2, and this ratio (ω) is approximated by Eq. 4. The approximations ρ_l and ρ_r always fall outside Region 2 (see Appendix), and ω overestimates the range of χ for which Region 2 exists (Fig. 3). Hence, the metric ω overestimates the actual risk predicted by the model. However, the accuracy of the approximations increases with high exotic competitive strength χ , when an invasive is of greatest concern.

The interpretation of ω is straightforward. Because all of the model parameters are positive, $\omega < 1$. For ω close to 1 (Fig. 3a), Region 2 occupies most of the area for $0 < \rho < \rho_r$, in which the exotic can invade. In this case, if the invader establishes a population, persistence of the native is unlikely unless the predator develops a strong preference for the exotic and moves the system into Region 3 ($\rho > \rho_r$). Region 2 narrows with decreasing ω (Fig. 3b) and disappears when $\omega = 0$ ($\rho_l = \rho_r$). If $\omega \leq 0$ (which occurs when $\rho_r < \rho_l$), Region 1 covers the entire area between χ_{\min} and χ_{\max} , and increasing predator preference for the exotic always benefits the native competitor. The range of χ spanned by Region 2 also increases with increasing ω (Fig. 3); therefore, large ω indicates high risk from an established exotic even if the relative competitive strength of the exotic is low.

Consumer conversion efficiencies are also critical components of competitive strength. Varying the consumer conversion efficiencies (ε_i) alters χ_{\max} as well as ω (see Appendix, Eq. A.4). For example, lowering the conversion efficiency of the exotic (ε_2) not only reduces ω but also increases χ_{\max} (Fig. 3c). Hence, in this scenario the exotic consumer must be a stronger resource competitor to exclude the native via direct resource competition. Changing the ε_i 's also alters ρ_r and therefore the "absolute" risk that the invasion poses. For example, if ρ_r is small then a relatively small increase in predator preference for the exotic will drive the exotic extinct (i.e., push the system into Region 3). Such an increase could occur if, for example, the predator evolved to attack the exotic more effectively.

The practical application of the results to an invasion scenario proceeds as follows. First, assess the invader's relative consumption rate: χ must be greater than χ_{\min} for the introduction to succeed. In this case, if the exotic is a superior resource competitor ($\chi > \chi_{\max}$), predation can not prevent extirpation of the native consumer. For $\chi_{\min} < \chi < \chi_{\max}$, predation on the invader can tip the balance from persistence to exclusion of the native consumer (from Region 1 to Region 2, Fig. 2). The risk of native extinction depends on the predator's preference for the exotic relative to the native consumer (ρ). Without knowing ρ beforehand, one can estimate the probability that the net effect of predation on the exotic will be extinction of the native from Eq. 4. For instance, in a highly productive system (large r , Fig. 3a) ω is close to 1 and predation on the exotic species poses a high risk to the native consumer. Alternatively, if the predator is relatively short lived (high d , Fig. 3b) ω is small and apparent competition is less likely to extirpate the native species.

DISCUSSION

Apparent competition increases the threat posed by an exotic competitor over a wide region of parameter space where direct resource competition alone would not exclude the native consumer ($\chi < \chi_{\max}$, Fig. 2). We have summarized this risk in a simple metric, ω , that bounds the fraction of predator preference values for which invasion is possible, and that results in extinction of the native competitor. The parameters in ω specify the pair-wise interactions in the food web and are measurable in the laboratory or field. Furthermore, one can estimate ω without previous knowledge of the predator's preference for the exotic relative to the native competitor (Eq. 4). Predator preference for the exotic may be difficult to estimate in the field during the early stages of an invasion, when the predator has had little experience with the new prey species.

The general theory that we have described is also applicable to a food web in which the predator is an exotic species. This case is particularly relevant to biological control, in which managers introduce a predator to reduce the impact of an exotic pest on a desirable native or crop species. Proper modern biological control requires safety tests to measure the host specificity of the biocontrol agent for the target pest species; however, biocontrol agents often attack some desirable, nontarget species as well (Pearson and Callaway 2003, Rand and Louda 2004, Stiling 2004). We can use our framework to address the question of how much relaxation of host specificity will spell extinction for the native species.

Perfect host specificity corresponds to zero preference for the native species. Hence, we reinterpret Fig. 2 with N_2 assigned to the native species and N_1 assigned to the invasive. In this case, the simple model (Eq. 1) predicts that the native species would be competitively excluded by the exotic in the absence of the biocontrol agent, P . Increasing ρ is now equal to increasing pref-

erence for the native consumer (i.e., weakening host specificity of the biocontrol agent). Similarly, χ measures the resource consumption rate of the native relative to the exotic consumer. The derived conditions are therefore reversed: exclusion of the native species now occurs in Region 3 of Fig. 2, and high ρ (predation on the native species) is particularly dangerous when ρ_r is small (low χ and $\varepsilon_2/\varepsilon_1$, which occurs when the native is a relatively weak competitor; see Eq. 3). The position of ρ_1 does not influence the extinction threat to the native species. In fact, decreasing ρ_1 may ultimately benefit the native species. For instance, a more productive system (higher r , Eq. 2) increases the relative size of Region 2 and thus the possibility that a low level of predation on the native will supplement the biocontrol agent and extirpate the pest via apparent competition (Fig. 3a). We do not interpret this result as reason to weaken standards for host specificity of biocontrol agents. Indeed, it would be difficult to estimate precisely the increase in ρ (decrease in host specificity) for a particular biocontrol agent that would place the system in Region 2 without risking the possibility that the additional predation extirpates the native (Region 3).

The metric ω and the exact analytic results in the Appendix and Fig. 2 are based on a simple model and require rigorous empirical testing. Several features of the model, such as predator and consumer functional responses, vary between systems and may influence the model predictions. Here we have employed the simplest possible model to highlight a problem that has not been integrated into the study of biological invasions, despite considerable attention from ecologists. Furthermore, we have demonstrated a general method to transfer the concept of apparent competition from community ecology to practical application in biological invasions. The general technique does not depend on the particular model that is appropriate for a given system.

A key feature of our approach is that we describe the coexistence boundaries in terms of predator preference, rather than the absolute attack rate on the exotic (b_2). Our goal is to estimate the extinction risk with minimal reference to the details of the full four-species system, which may be difficult to ascertain until it is too late to intervene. Courchamp et al. (2000) addressed a similar problem with a model of two consumers with a shared predator but distinct resources (i.e., only apparent competition). Courchamp et al. (2000) modeled the indirect link between the two prey with a preference function in the predator's functional response; otherwise, their model is identical to that of Holt (1977). However, describing preference requires some care. Courchamp et al. (2000) assumed a predator functional response of the form $(e_1 b_1 \alpha N_1^2 + e_2 b_2 N_2^2) / (\alpha N_1 + N_2)$, where $\alpha \geq 1$ is the measure of preference for the more preferred prey, N_1 (we have converted the other parameters to our notation). This functional response decreases with increasing abundance of the pre-

ferred prey (negative derivative with respect to N_1) when $e_1 b_1 N_1 (\alpha N_1 + 2N_2) / e_2 b_2 N_2^2 < 1$. Hence the model displays the unrealistic behavior that increasing the abundance of the preferred prey (N_1) decreases the functional response if the less preferred prey (N_2) is sufficiently abundant. Indeed, the nonmechanistic form of the preference function (in particular, the possibility of a zero in the denominator) in their model appears to be the source of the additional complexity that Courchamp et al. (2000) confronted in their analysis.

Ecologists are increasingly recognizing the importance of integrating community ecology theory with the study of biological invasions (Holt and Hochberg 2001, Shea and Chesson 2002, Byers and Noonburg 2003, Pearson and Callaway 2003). Here we have developed one avenue for transfer of basic ecological understanding to applications in invasion biology as well as biological control. The study of biological invasions can also provide new insight into the fundamental issues surrounding community structure and dynamics. The simple model discussed here not only serves as a tool for managing invasions, but also makes testable predictions about the consequences of introduced species for the native community.

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LITERATURE CITED

- Abrams, P. A. 1993. Effect of increased productivity on the abundances of trophic levels. *American Naturalist* **141**:351–371.
- Abrams, P. A. 2004. Trait-initiated indirect effects due to changes in consumption rates in simple food webs. *Ecology* **85**:1029–1038.
- Armstrong, R. A. 1979. Prey species replacement along a gradient of nutrient enrichment: a graphical approach. *Ecology* **60**:76–84.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* **115**:151–170.
- Baltz, D. M., and P. B. Moyle. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecological Applications* **3**:246–255.
- Byers, J. E. 2002. Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia* **130**:146–156.
- Byers, J. E. 2005. Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology* **86**:487–500.
- Byers, J. E., and E. G. Noonburg. 2003. Scale dependent effects of biotic resistance to biological invasion. *Ecology* **84**:1428–1433.
- Chase, J. M., P. A. Abrams, J. P. Grover, S. Diehl, P. Chesson, R. D. Holt, S. A. Richards, R. M. Nisbet, and T. J. Case. 2002. The interaction between predation and competition: a review and synthesis. *Ecology Letters* **5**:302–315.
- Chesson, J. 1978. Measuring preference in selective predation. *Ecology* **59**:211–215.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* **64**:1297–1304.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* **31**:343–366.
- Courchamp, F., M. Langlais, and S. Sugihara. 2000. Rabbits killing birds: modelling the hyperpredation process. *Journal of Animal Ecology* **69**:154–164.
- Elton, C. 1958. *The ecology of invasions by animals and plants*. Wiley, New York, New York, USA.
- Grover, J. P., and R. D. Holt. 1998. Disentangling resource and apparent competition: realistic models for plant–herbivore communities. *Journal of Theoretical Biology* **191**:353–376.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* **12**:197–229.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. *American Naturalist* **144**:741–771.
- Holt, R. D., and M. E. Hochberg. 2001. Indirect interactions, community modules and biological control: a theoretical perspective. Pages 13–38 in E. Wajnberg, J. K. Scott, and P. C. Quimby, editors. *Evaluating indirect ecological effects of biological control*. CAB International, Wallingford, UK.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* **61**:65–71.
- Leibold, M. A. 1989. Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *American Naturalist* **134**:922–949.
- Leibold, M. A. 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* **147**:784–812.
- Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* **7**:975–989.
- Pearson, D. E., and R. M. Callaway. 2003. Indirect effects of host-specific biological control agents. *Trends in Ecology and Evolution* **18**:456–461.
- Rand, T. A., and S. M. Louda. 2004. Exotic weed invasion increases the susceptibility of native plants attack by a bio-control herbivore. *Ecology* **85**:1548–1554.
- Robinson, J. V., and G. A. Wellborn. 1988. Ecological resistance to the invasion of a freshwater clam, *Corbicula fluminea*: fish predation effects. *Oecologia* **77**:445–452.
- Roemer, G. W., T. J. Coonan, D. K. Garcelon, J. Bascompte, and L. Laughrin. 2001. Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox. *Animal Conservation* **4**:307–318.
- Shea, K., and P. Chesson. 2002. Community ecology as a framework for biological invasions. *Trends in Ecology and Evolution* **5**:302–315.
- Stiling, P. 2004. Biological control not on target. *Biological Invasions* **6**:151–159.
- Trowbridge, C. D. 1995. Establishment of the green alga *Codium fragile* ssp. *tometosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. *Journal of Ecology* **83**:949–965.
- Wajnberg, E., J. K. Scott, and P. C. Quimby. 2001. *Evaluating indirect ecological effects of biological control*. CAB International, Wallingford, UK.

APPENDIX

Coexistence conditions and derivation of ω are available in ESA's Electronic Data Archive: *Ecological Archives* E086-137-A1.