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Nonrandom extinction patterns can modulate pest control service decline

DANIEL S. KARP,[1,2,3] HOLLY V. MOELLER,[2] AND LUKE O. FRISHKOFF[1,2]

[1]*Center for Conservation Biology, Stanford University, Stanford, California 94305 USA*
[2]*Department of Biology, Stanford University, Stanford, California 94305 USA*

Abstract. Changes in biodiversity will mediate the consequences of agricultural intensification and expansion for ecosystem services. Regulating services, like pollination and pest control, generally decline with species loss. In nature, however, relationships between service provision and species richness are not always strong, partially because anthropogenic disturbances purge species from communities in nonrandom orders. The same traits that make for effective service providers may also confer resistance or sensitivity to anthropogenic disturbances, which may either temper or accelerate declines in service provision with species loss. We modeled a community of predators interacting with insect pest prey, and identified the contexts in which pest control provision was most sensitive to species loss. We found pest populations increased rapidly when functionally unique and dietary-generalist predators were lost first, with up to 20% lower pest control provision than random loss. In general, pest abundance increased most in the scenarios that freed more pest species from predation. Species loss also decreased the likelihood that the most effective service providers were present. In communities composed of species with identical traits, predators were equally effective service providers and, when competing predators went extinct, remaining community members assumed their functional roles. In more realistic trait-diverse communities, predators differed in pest control efficacy, and remaining predators could not fully compensate for the loss of their competitors, causing steeper declines in pest control provision with predator species loss. These results highlight diet breadth in particular as a key predictor of service provision, as it affects both the way species respond to and alter their environments. More generally, our model provides testable hypotheses for predicting how nonrandom species loss alters relationships between biodiversity and pest control provision.

Key words: agriculture; biodiversity; ecosystem function; ecosystem services; extinction; nonrandom species loss; pest control; predator–prey models; species loss.

INTRODUCTION

As human activity continues to erode biodiversity, the function of Earth's life-support systems will largely depend on which organisms survive (Balvanera et al. 2006, Barnosky et al. 2011). In particular, future provision of biotic ecosystem services will be mediated by the ability of ecosystem-service providers to persist as agriculture expands and intensifies to support the burgeoning human population (Tilman et al. 2001, Bianchi et al. 2006, Ricketts et al. 2008, Letourneau et al. 2009). The value of biotic services like crop pollination and pest control to society is great; farm yields and revenues are significantly enhanced by native pollinators and predators of crops pests (Kellermann et al. 2008, Ricketts et al. 2008, Klein et al. 2009, Boyles et al. 2011).

The insectivorous species potentially responsible for such pest control services are in decline, unable to cope with the changes in habitat that accompany the intensification and expansion of agriculture (Canaday 1996, Tscharntke et al. 2008, Karp et al. 2011). This lowered insectivore diversity may result in higher pest abundances (Wilby and Thomas 2002, Cardinale et al. 2003, Casula et al. 2006, Snyder et al. 2006, Straub and Snyder 2006, Van Bael et al. 2008, Philpott et al. 2009). First, predators in diverse communities may act complementarily, in that different predator species consume different suites of pest prey. In such systems, the loss of insectivore species may result in the escape of their prey from predation, thereby reducing pest control services (Hooper et al. 2005). Second, more diverse communities may be more likely to contain the most effective predators. The greater the declines in insectivore diversity, the greater the likelihood that these particularly effective predators are lost (Straub and Snyder 2006). Regardless of mechanism, the decline in biodiversity with agricultural intensification is expected to reduce pest control provision.

Linking insectivore diversity and pest control provision, however, is not always straightforward (Bianchi et al. 2006, Van Bael et al. 2008). One potential explana-

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[3] E-mail: dkarp@stanford.edu

tion may be that, in reality, species are not lost from communities randomly. Processes such as agricultural expansion and intensification preferentially purge species with a distinct set of traits (Lindell et al. 2004, Tscharntke et al. 2008), in turn altering relationships between diversity and ecosystem-service provision (Zavaleta and Hulvey 2004, Kremen 2005, Larsen et al. 2005, Bracken et al. 2008). The same functional traits that confer species persistence (response traits) may simultaneously mediate service provision (effect traits), modifying relationships between disturbances and service provision (Zavaleta and Hulvey 2004, Kremen 2005, Larsen et al. 2005). For example, large-bodied bees are both more effective pollinators and more sensitive to land use intensification than small bees (Kremen 2005, Larsen et al. 2005). Provision of pollination (Larsen et al. 2005), decomposition (Larsen et al. 2005), invasion resistance (Zavaleta and Hulvey 2004), nutrient uptake (Bracken et al. 2008), sediment bioturbation (Solan et al. 2004), disease regulation (Ostfeld and LoGiudice 2003), and carbon sequestration (Bunker et al. 2005) services decline more rapidly in nature than would be expected if species loss were random.

Alternatively, correlations between response and effect traits may temper the consequences of species loss for ecosystem function. For example, dietary generalists often persist in human-dominated landscapes (Lindell et al. 2004, Tscharntke et al. 2008) and may exert stronger top-down control on prey abundance than specialists (Symondson et al. 2002, Jiang and Morin 2005, Bianco Faria et al. 2008). Because they consume a wider range of prey items, generalists may be more likely to consume prey that have no other predators. Specialists may therefore be more redundant than generalists, and the persistence of generalists may dampen the effects of land use intensification on service provision.

To develop a theoretical framework for how nonrandom species loss patterns could alter the relationship between biodiversity and pest control provision, we modeled a bitrophic community of pests and their predators (Volterra 1926, Ives et al. 2005). We did not parameterize our model for specific predator taxa so that our model could be applied to a variety of predator–pest communities. Using our model, we tested the effects of nonrandom species loss patterns on community-level pest control provision. We compared the preferential loss of (1) generalist, (2) specialist, (3) functionally unique, (4) functionally redundant, and (5) rare predator species to a null model of random species loss. We also explored the mechanisms through which diversity may enhance pest control provision, and alter rates of pest control decline among the nonrandom species loss scenarios. We found that nonrandom species loss may have profound effects on service provision, underscoring the importance of linking response and effect traits to our understanding of continued ecosystem function.

METHODS

Model structure and simulations

We independently generated 25 communities consisting of 30 predator species (consumers, C_i), and 20 prey species, P_j. We chose to include more predators than prey to ensure that most prey items were consumed by at least one predator. Regardless, our model can be adapted to accommodate different numbers of predators and prey. In each community, we randomly assigned four prey species to be agricultural pests and the rest to be non-pest prey. Predators (C) and prey (P) interacted according to the dynamical equations:

$$\frac{dP_j}{dt} = r_j P_j\left(1 - \frac{P_j}{K_j}\right) - \sum_{i=1}^{C} \frac{\frac{a_{ij}}{g_i} P_j C_i}{1 + \sum_{k=1}^{P} h_{ik} P_k}$$

$$\frac{dC_i}{dt} = \frac{\sum_{j=1}^{P} \frac{b_{ij} a_{ij}}{g_i} P_j}{1 + \sum_{k=1}^{P} h_{ik} P_k} C_i - m_i C_i. \qquad (1)$$

Prey grew logistically at a species-specific rate, r_j, to a carrying capacity, K_j. Predation followed a competitive Holling Type II functional response (Holling 1959), with an interaction-specific attack rate of predator i on prey j, a_{ij}, and handling time by predator i of prey k, h_{ik}. Thus, as prey abundance increased, predation rate increased to a threshold (a_{ij}/g_j), but the marginal increase in predation rate declined with increasing abundance of all consumed prey types. Allowing attack rates to increase with prey abundance opened the possibility for behaviors similar to prey switching. As predators were lost, remaining predators could increase their attack rates on abundant prey that were partially released from predation. In this way, predators could respond to changes in prey abundances and adjust their feeding behavior. Predator biomass increased as a function of predation activity, with conversion efficiency from prey j to predator i of b_{ij}. Predators died at a fixed mortality rate, m_j.

Attack rates were normalized to diet breadth (i.e., number of prey species eaten by the predator) g_i, to account for a trade-off between diet breadth and per-species attack rate (Bianco Faria et al. 2008); specialists were more effective at hunting their prey than generalists (Bernays and Funk 1999). We modeled the diet breadth distribution of each community of predators in two ways. In a first set of simulations, diet breadths were Poisson distributed ($\lambda = 1$), meaning specialists were more common than generalists, a situation that may be observed in the tropics (Dyer et al. 2007). Indeed, specialists were more common than generalists in three studies with 14 parasitoid–prey food webs (Henneman and Memmott 2001, Albrecht et al. 2007, Tylianakis et al. 2007; Appendix: Fig. A1). Regardless, we accounted for the possibility that specialists and generalists are equally common in a second set of simulations in which diet breadths were uniformly distributed (where g_i ranged from 1 to 5). In order to assign predators their prey, we ordered prey arbitrarily along a circular trait axis, which could represent variation in one or a combination of traits not explicitly described by the model (Appendix: Fig. A2). Specialists ($g = 1$) were randomly assigned a single prey species; generalists were assigned a set of functionally similar (adjacent on the trait axis) prey species. Where no link existed between a predator, i, and prey species, j (i.e., the consumer did not eat that prey item), $a_{ij} = h_{ij} = 0$. Our random assignment of pests to predators, and large number of predator species, generated competition within communities (when two or more predators consumed the same pest species). This competition allowed for two forms of compensation to take place when a predator species went extinct: (1) functional compensation, in which predator attack rates instantaneously increased on prey that were released from competitor predation, and (2) numerical compensation, in which the equilibrium abundance of the remaining predators increased (Touchton and Smith 2011).

All parameters except diet breadth were independently sampled from normal distributions with mean values of $b_{ij} = 0.1$, $a_{ij} = 0.067$, $h_{ij} = 0.0067$, $K_j = 500$, $m_i = 0.5$, and $r_j = 1$, parameter values that produce a stable equilibrium for a two-species system. We varied the standard deviation of the normal distribution to simulate variation in life histories and, therefore, varying levels of community-level trait diversity. Here, we show results from standard deviations equal to 0% (no trait diversity), 10% (low trait diversity), and 25% (high trait diversity) of mean values.

For each community, we used MATLAB (MATLAB 2009) to find the equilibrium abundances of prey and predators when all species were present. We then studied the consequences of differing scenarios of predator species loss. Though agricultural practices often directly alter prey communities alongside predator communities, we focused our simulations only on predator species loss for simplicity. Allowing prey species richness to change would obscure direct relationships between nonrandom predator species loss and pest control provision, the object of our study. Furthermore, assuming constant prey species richness may not be entirely unrealistic; changes in coffee farm management in Jamaica were shown to have substantial implications for birds and canopy-dwelling arthropods, but not coffee-dwelling arthropods (Johnson 2000).

Species were chosen randomly for random loss scenarios. For rare, generalist, and specialist loss scenarios, we ordered predators according to their abundance or diet breadth, and then used a Poisson distribution ($\lambda = 1$) to choose which species would be preferentially lost from the community (Appendix: Fig. A2). For functionally unique and functionally redundant species loss scenarios, we examined which pest had the fewest predators, and defined the predators of these species as the most functionally unique. We again used a Poisson distribution to preferentially choose functionally unique or functionally redundant (the inverse order of functionally unique) species for loss (Appendix: Fig. A2). Because specialists and generalists were randomly assigned to prey, generalists on average consumed more unique prey items than specialists and were therefore more likely to be functionally unique. For each loss scenario, we simulated the effects of eight loss severities: losing 1 (3% of species), 2 (~5%), 3 (10%), 5 (~15%), 6 (20%), 8 (~25%), 9 (30%), and 15 (50%) predator species. For each loss severity, we ran 10 simulations, for a total of 80 simulations per loss pattern, per community.

Statistical analysis

For each community prior to deleting species, we randomly designated four prey items as agricultural pests and computed their reductions from carrying capacity after all iterations of species loss. We repeated this process a total of 10 times with a different random realization of pests each time. We then took the average reduction from carrying capacity of the 10 random realizations as our final measure of pest control provision. For each community ($n = 25$) and species loss scenario ($n = 6$), we then extracted the slopes of the best-fit lines (ordinary least squares) that related the proportion of predator species lost to pest reduction from carrying capacity. The slopes were used as a measure of the sensitivity of pest control provision to species loss. We compared these slopes among species loss scenarios with analysis of variance (ANOVA) and Tukey post hoc planned contrasts. In simulations where residuals were not normally distributed, we used Kruskal-Wallis nonparametric tests with planned Wilcoxon contrasts to examine differences in slope.

We investigated mechanisms by which more diverse predator communities could better reduce pest abundances. First, we assessed whether more diverse communities were more likely to contain species that consumed the full array of pests. For each simulation, we calculated pest coverage or the proportion of the four pests that had at least one predator present. Then, for each constructed community and species loss scenario, we extracted the slopes from the best-fit lines relating pest coverage to the proportion of predator species lost. Again, we compared slopes among species loss scenarios with ANOVA when residuals were normally distributed and with Kruskal-Wallis nonparametric tests when residuals were not normally distributed. Next, we examined how well pest coverage predicted pest reduction from carrying capacity. Because multiple simulations were run for each predator loss severity, many simulations for the

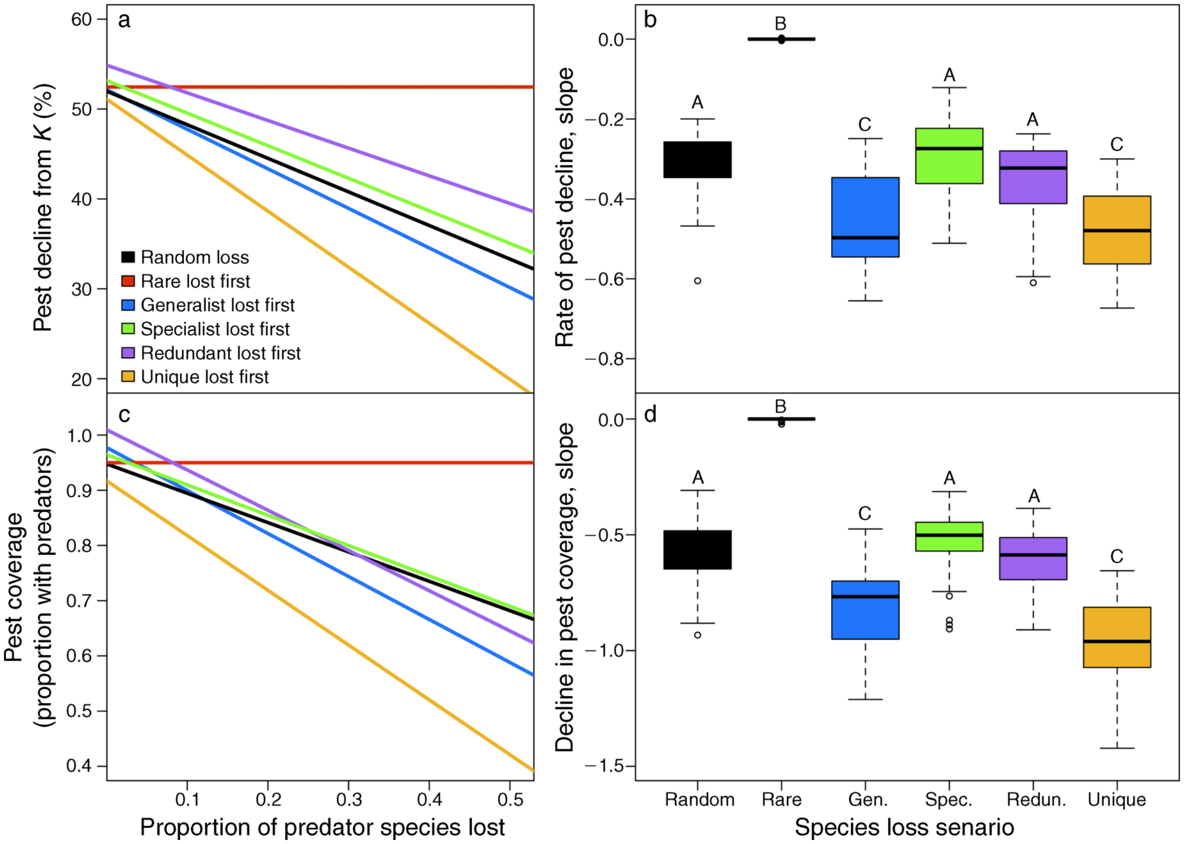

FIG. 1. Nonrandom loss alters the sensitivity of pest control to species loss. (a) Average pest percentage reduction from carrying capacity, *K*, as a function of predator loss for one example community. (b) The rate of pest decline varies by predator loss scenario (random loss, rare species lost first, generalists lost first, specialists lost first, redundant species lost first, unique species lost first). Plots show the slopes relating the proportion of predators lost to pest percentage decline from carrying capacity. (c) The influence of predator species loss on pest coverage (proportion of the four pest species with predators present). (d) Decline in pest coverage [slopes from panel (c)] as a function of the loss scenario. Different uppercase letters above box plots in panels (b) and (d) denote significance ($P < 0.05$) under Wilcoxon contrasts. Box plots depict the median (line in box), the upper and lower quartiles (bounds of the box), the range of the data (whiskers), and outliers (circles).

same community resulted in the same prey coverage. To avoid using each simulation as a pseudo-replicate, we averaged the pest reduction from carrying capacity for all simulations of the same community that resulted in the same pest coverage. We then regressed pest reduction from carrying capacity against pest coverage using simulated communities ($n = 25$) as replicates.

We also investigated whether increasing the number of predator species present reduces the abundance of their single shared prey species. This could occur if diversity increases the likelihood that the most effective predator is present. For every pest species that had at least four predators, we calculated its percentage reduction from carrying capacity when one, two, three, four, and (potentially) five of its predators were present. The predator that reduced the pest's abundance the most (relative to its carrying capacity) when it was the only predator present was termed the "most effective predator"; this is analogous to the R* concept, in that the most effective predator has the lowest R* (Tilman 1982). We also compared the percentage decline of a pest when its most effective predator was present to its percentage decline when two to five of its other predators were present.

Finally, we assessed the degree to which, when a predator is lost from a community, remaining extant predators compensated for its loss by increasing in abundance. We averaged the abundance of all remaining predators in the community after species were lost, and then extracted the slopes of the best-fit lines (ordinary least squares) that related the proportion of predators lost to average abundance of remaining predators. We then compared compensation among communities of varying levels of trait diversity with ANOVA to evaluate the hypothesis that communities with more niche differentiation (and thus less competition) exhibit less compensation.

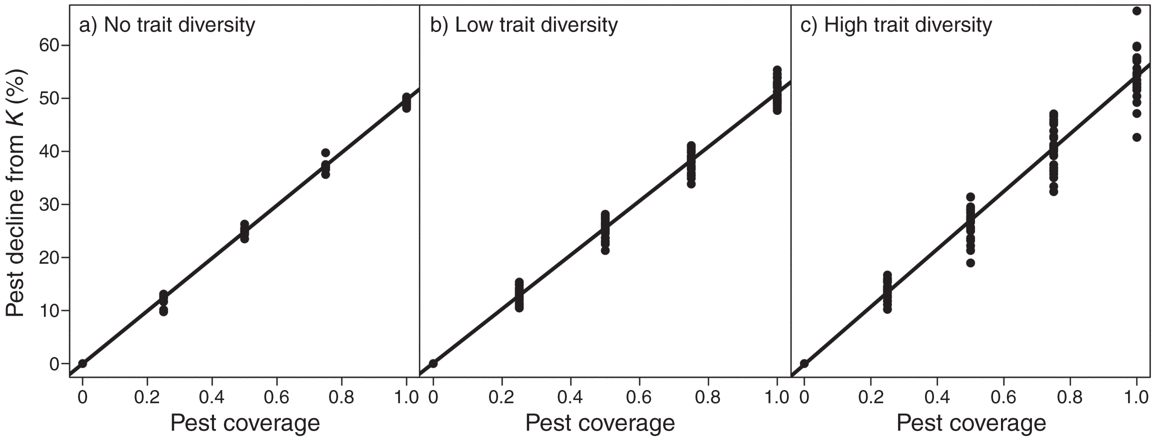

FIG. 2. Pest coverage (proportion of pests with predators present) strongly predicts pest control provision (average percentage decline from carrying capacity among all four pests). Only random species loss scenarios are used, and pest coverage is averaged within communities to avoid pseudoreplication. Pest coverage explained less variation in pest control in high-trait-diversity communities than in low-trait-diversity communities. (a) Simulations in which all predators and prey have the same traits (no trait diversity). (b, c) Simulations with low and high trait diversity (model parameters vary with parameter standard deviations equal to 10% and 25% of parameter mean values, respectively).

RESULTS

Nonrandom species loss

Intact predator communities reduced total pest abundance by ~50% relative to pest carrying capacity (Fig. 1a). For all scenarios, predator extinction led to reductions in pest control provision, though the magnitude and rate of these declines depended significantly upon the pattern of species loss ($\chi^2 = 86.9$, df = 5, $P < 0.01$; Fig. 1 a, b). In particular, preferential loss of generalist and functionally unique species led to more rapid declines in pest control services (increasing pest abundances) than random species loss ($P < 0.01$). Similarly, the relationship between diversity and pest control provision was most predictable (R^2 values were highest) when generalists and functionally unique species were lost first ($F = 38.8$, df = 5, 144, $P < 0.01$). The loss of specialist and functionally redundant species produced results comparable to random species loss ($P = 0.31$, $P = 1$, respectively). By contrast, preferential loss of rare species affected pest control services less than random loss ($P < 0.01$), likely because predators with small population densities contribute less to service provision than more abundant community members (Solan et al. 2004). In fact, pest control did not decline appreciably as rare species were lost, indicating that some species were not abundant enough to regulate pest populations. These results were robust to the amount of variation in model parameters (Appendix: Fig. A3a, b, c, d). Further, results did not differ for communities with uniformly distributed diet breadths (which resulted in higher abundance of generalists), with the exception that losing specialists first caused less sensitivity to species loss than random species loss scenarios ($P < 0.01$; Appendix: Fig. A3e, f).

Drivers and mechanisms

Pest coverage, the proportion of prey with at least one predator present, predicted pest control provision (Fig. 2), and pest coverage decreased with predator loss (Fig. 1c, d). Further, pest-coverage decline rates differed among species loss scenarios, following the same pattern as pest control rates ($F = 89.8$, df = 5, 144, $P < 0.01$; Fig. 1c, d). For example, losing generalists and functionally unique species first resulted in a more rapid decline in pest coverage than the other species loss scenarios ($P < 0.01$). Qualitative relationships among species loss scenarios did not change with community trait diversity (Appendix: Fig. A4); however, increasing community-wide trait diversity decreased the amount of variance that prey coverage explained in pest control provision (Fig. 2).

For simulations with no community-level trait diversity, large gains in pest control were achieved when a pest went from having no predators to having one. Yet, the addition of subsequent predators after the first did not enhance pest control (Fig. 3a). By contrast, when traits varied, the presence of additional predators increased pest control incrementally (Fig. 3b, c), likely because trait diversity resulted in different functional effectiveness of each predator. Further, a pest's abundance when its most effective predator was present was equivalent to its abundance when the most diverse predator assemblage was present (Fig. 3; $W = 1000.5$, $P = 0.19$).

Increasing species trait diversity also caused a decrease in compensatory changes in abundance among predators. In communities with no trait diversity, the abundance of remaining predators increased rapidly after the extinction of their competitors (Fig. 4). Once traits were allowed to vary, the abundance of remaining predators increased at a significantly slower rate ($F = 36$, df = 2, 72, $P < 0.01$; Fig. 4). This, in part, contributed to

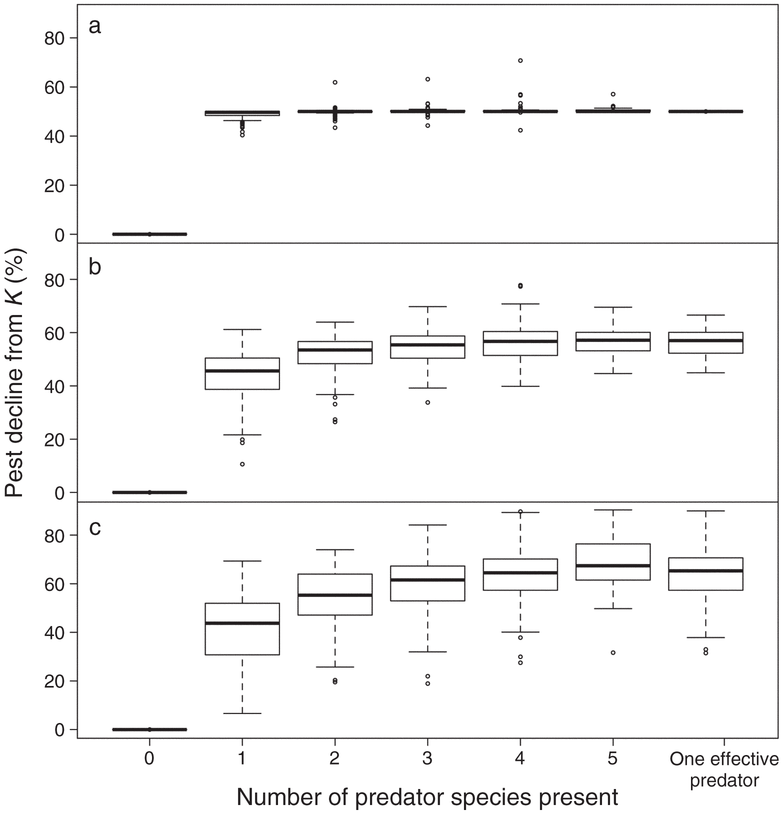

FIG. 3. Effect of the number of predators present on pest percentage decline from carrying capacity. (a) Simulations in which all predators and prey have the same traits. (b, c) Simulations with low and high trait diversity (predator and prey traits vary with parameter standard deviations equal to 10% and 25% of mean values, respectively). In simulations with no trait diversity, effects of predator loss on service provision stem from trophic release of pest species. In communities where consumers differ, incremental increases in predation pressure on individual pest species improve pest control provision. In all cases, average prey reduction is equivalent when one "best predator" is present and when five predator species are present. Box plot components are as in Fig. 1.

higher sensitivity of pest control provision to species loss in communities with higher trait diversity ($\chi^2 = 27.7$, df = 2, $P < 0.01$; Fig. 5).

DISCUSSION

Though it is possible that species loss could reduce competitive interactions between effective pest control providers, our model supports the growing body of observations and experiments that affirm pests increase in abundance as predator biodiversity declines (Cardinale et al. 2003, Snyder et al. 2006, Straub and Snyder 2006, Van Bael et al. 2008, Letourneau et al. 2009, Philpott et al. 2009*b*) More interestingly, we report that the rate of pest control decline may depend strongly on the identity of predator species lost. In particular, our results highlight the importance of maintaining pest coverage as predators are lost from biological communities. Preferential loss of functionally unique species resulted in a rapid decline in pest control service provision, a result consistent with studies of other services (Zavaleta and Hulvey 2004). It is unclear whether functionally unique species are preferentially lost from biological communities in nature; however, there is some evidence that land use intensification purges functional diversity from biological communities rapidly (Flynn et al. 2009). Given the lack of study in this area, our model indicates that assessing the degree to which functional complementarity is maintained as species are lost should be a key research priority.

Our model also demonstrated diet breadth to be a key predictor of ecosystem service provision, likely because generalists were more functionally unique in our model than specialists. Therefore, pest control declined significantly faster when generalists were lost before specialists, suggesting that preferential loss of specialists could temper declines in service provision, especially in communities with equal numbers of generalists and specialists (Appendix: Fig. A3e, f). Moreover, the relationship between diversity and service provision was most reliable when generalists and functionally unique species were lost first. The relationship between diet breadth and functional uniqueness in our model derived from random assignment of predators to prey. Generalists, by definition, consumed more prey species and were therefore more likely to consume more unique prey items.

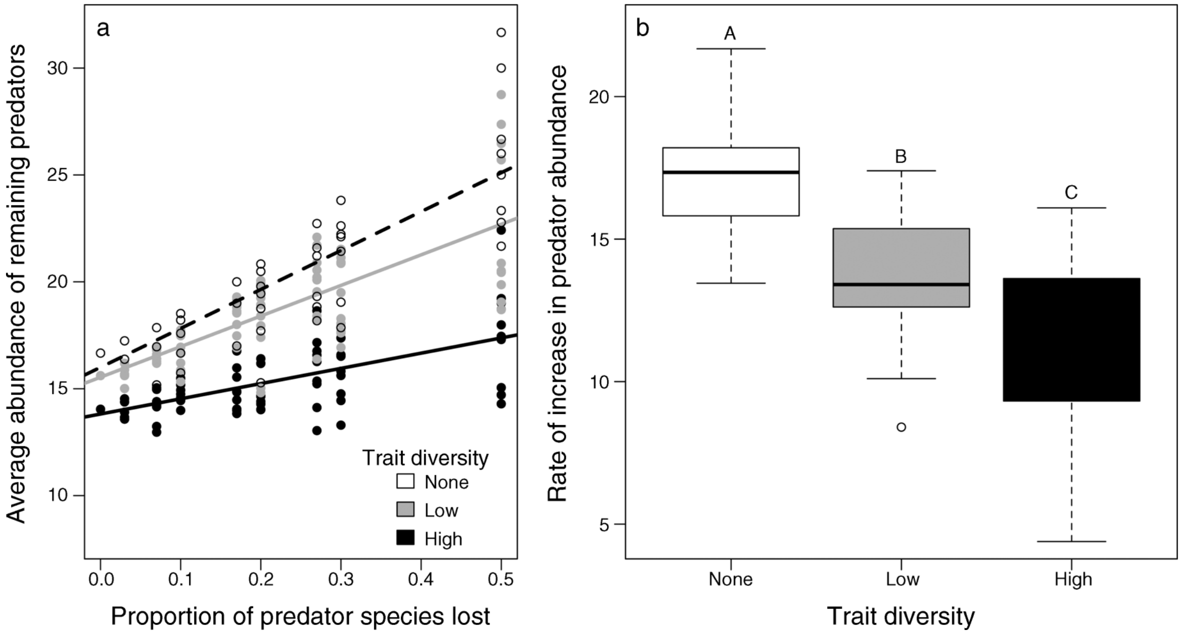

FIG. 4. Compensatory changes in abundance for remaining predators after loss of their competitors. (a) The average abundance of remaining predators increases with the proportion of predator species lost at three levels of trait diversity. (b) The rate of increase in remaining predator abundance [slopes from panel (a)] as a function of predator trait diversity. Increasing trait diversity results in a decrease in compensatory changes in abundance. Different uppercase letters above box plots in panel (b) denote significance ($P < 0.05$) under Tukey post hoc contrasts. Box plot components are as in Fig. 1.

Though not well investigated, the connection between diet breadth and functional uniqueness may be realistic. We obtained 14 food webs from three studies investigating parasitoid–herbivore interactions in tropical and temperate landscapes (Henneman and Memmott 2001, Albrecht et al. 2007, Tylianakis et al. 2007). For each food web, we assessed how parasitoid functional uniqueness varied with diet breadth by examining all parasitoids with a given diet breadth and calculating the fraction of their prey species for which they were the only predator. We did not find a relationship between the probability that prey were eaten by a single predator and that predator's diet breadth ($R^2 = 0.02$, $P = 0.35$; Appendix: Fig. A5a). In other words, a prey species consumed by a specialist was as likely to be eaten by only one predator as a prey species assigned to a generalist, supporting the

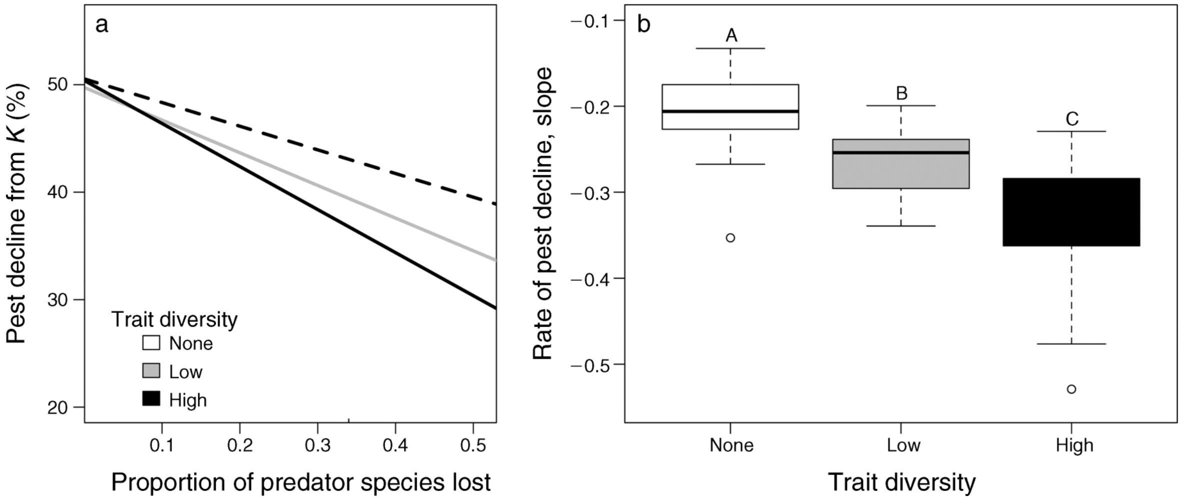

FIG. 5. Pest control is most sensitive to species loss in functionally diverse communities. (a) Pest decline from carrying capacity as a function of consumer loss for one simulated community at three levels of trait diversity. (b) The rate of pest control decline [slopes from panel (a)] increases with predator trait diversity. Different uppercase letters above box plots in panel (b) denote significance ($P < 0.05$) under Wilcoxon signed rank contrasts. Box plot components are as in Fig. 1.

PLATE 1. Predicting changes in pest-control provision may require assessments of predators' diet breadths, as diet breadth regulates predators' responses to disturbances and their effects on pests. For example, (left) the Barred Antshrike (*Thamnophilus doliatus*), a generalist insectivore, thrives in human-dominated landscapes and may suppress pests better than (right) the Rufous-tailed Jacamar (*Galbula ruficauda*), a flying insect specialist that is largely restricted to forest. Photo credits: D. S. Karp.

random attribution of predators to prey in our model. Additionally, we tallied the number of unique prey items for each predator, and found a significant positive relationship between this measure of functional uniqueness and diet breadth ($R^2 = 0.57$, $P < 0.01$; Appendix: Fig. A5b). Thus we conclude that our model design mimics real food web structure, with increased functional uniqueness of generalists stemming from their multiple random draws (i.e., one "draw" per species consumed) from a pool of prey species.

Field data and models also validate that generalists are important pest control providers, exerting strong top-down control on their prey (Provencher and Riechert 1994, Symondson et al. 2002, Jiang and Morin 2005, Bianco Faria et al. 2008). Moreover, because predator species differ in foraging strategies and prey preferences, high generalist species richness is associated with low community-wide prey abundances (Provencher and Riechert 1994). Dietary generalists are also better able to persist in highly modified landscapes than specialists (Lindell et al. 2004, Tscharntke et al. 2008) and are less extinction prone (Boyles and Storm 2007, Colles et al. 2009). This may be due to a lack of sensitivity to population fluctuations in any individual prey species (Boyles and Storm 2007), an ability to transition to alternative prey species as competitors are lost, and/or intrinsic correlations between diet breadth and other traits, for example habitat breadth (Sloggett and Majerus 2000). Therefore, diet breadth may be a key predictor of ecosystem-service provision because, like body size (Larsen et al. 2005), it functions both as a response trait (mediating resilience to disturbance) and an effect trait (mediating impact on ecosystem function; see Plate 1).

Pest coverage, however, was not the only mechanism driving strong relationships between diversity and service provision. Retaining additional predators served to incrementally depress abundances of individual pest species (Straub and Snyder 2006). When traits varied, certain trait combinations (e.g., high attack rates and conversion efficiencies) made some species more effective predators and thus, more effective pest control providers than others, even when preying upon the same pest species. Thus, maintaining predator diversity increased the likelihood that the most effective predators were present. Because real-world biological communities will more closely resemble the trait-variable communities modeled here, our results highlight the potential importance of functional redundancy to the regulation of individual pest species.

Community trait diversity also influenced the degree to which predators exhibited compensatory increases in abundance. In simulations where predator traits were fixed (i.e., every predator was identical except for differences in diet breadth), surviving predators rapidly increased in abundance as their competitors were lost. By contrast, trait-diverse communities exhibited reduced numerical compensation. Lower numerical compensation likely caused pest control services to be more sensitive to species loss in trait-diverse communities than in fixed-parameter communities. Further, numerical compensation appears to be relatively rare in nature (Houlahan et al. 2007, Valone and Barber 2008, Winfree and Kremen 2009), even for functionally similar species (Karp et al. 2011). Therefore, real communities are more likely to exhibit the heightened sensitivity to species loss characteristic of trait-diverse communities than the comparative resilience characteristic of fixed-parameter communities.

It is important to note that in all analyses, we focused on equilibrium pest abundances, ignoring transient pest population dynamics. "Transient" community dynamics can in fact endure for long periods of time (Fukami and Nakajima 2011), and temporary pest population increases (outbreaks) are of obvious importance to farmers. Theory suggests that generalists stabilize pest suppression more than specialists, but sustained pest suppression may be maximized in communities composed of both specialists and generalists (Bianco Faria et al. 2008). Especially because predators have been shown to prevent pest outbreaks and stabilize ecosystem function (Perfecto et al. 2004), future theoretical investigation into the consequences of nonrandom predator loss for transient pest population dynamics is needed.

Ultimately, declines in ecosystem-service provision will depend upon the patterns of species loss and particulars of the ecosystem in question. While real communities are more likely to resemble trait-diverse than fixed-parameter communities, the degree of pest control resilience to species loss will strongly depend on the identity of species lost. Indeed, our results showed that the loss of half of the same predator community can cause a decline in pest control services by as little as 8% when specialist species are lost first, but by as much as 27% when generalists are lost first. Future empirical work would profitably focus on the prevalence and significance of losing functionally unique and generalist species to clarify whether or not nonrandom species loss accentuates or tempers pest control provision in nature. Regardless, the simplicity of our model and our generic approach have allowed us to characterize a suite of functional patterns controlling the provision of pest control services, and provide a framework of hypotheses readily testable by field data.

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Supplemental Material

Appendix

Five figures that illustrate model procedures, show model sensitivity analyses, and compare results to observations in published predator–prey interaction webs (*Ecological Archives* A023-042-A1).