

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Faculty Publications in the Biological Sciences

Papers in the Biological Sciences

2020

Towards understanding factors influencing the benefit of diversity in predator communities for prey suppression

Amanda N. Laubmeir

Richard Rebarber

Brigitte Tenhumberg

Follow this and additional works at: <https://digitalcommons.unl.edu/bioscifacpub>

 Part of the [Biology Commons](#)

This Article is brought to you for free and open access by the Papers in the Biological Sciences at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Faculty Publications in the Biological Sciences by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.



Towards understanding factors influencing the benefit of diversity in predator communities for prey suppression

AMANDA N. LAUBMEIER,^{1,3} RICHARD REBARBER,¹ AND BRIGITTE TENHUMBERG^{1,2,†}

¹Department of Mathematics, University of Nebraska–Lincoln, 203 Avery Hall, PO BOX 880130, Lincoln, Nebraska 68588-0130 USA

²School of Biological Sciences, University of Nebraska–Lincoln, 402 Manter Hall, 1104 T Street, Lincoln, Nebraska 68588-0118 USA

Citation: Laubmeier, A. N., R. Rebarber, and B. Tenhumberg. 2020. Towards understanding factors influencing the benefit of diversity in predator communities for prey suppression. *Ecosphere* 11(10):e03271. 10.1002/ecs2.3271

Abstract. It is generally assumed that high biodiversity is key to sustaining critical ecosystem services, including prey suppression by natural predator guilds. Prey suppression is driven by complex interactions between members of predator and prey communities, as well as their shared environment. Because of this, empirical studies have found both positive and negative effects of high predator diversity on prey suppression. However, we lack an understanding of when these different prey suppression outcomes will occur. In this work, we use a mechanistic, trait-based model to unravel how intraguild interactions, species body mass, predator foraging area, and ambient temperature can combine to produce different levels of prey suppression. Surprisingly, we find that prey suppression is only improved by high biodiversity under a limited set of conditions. The most important factor in determining whether diversity improves prey suppression is the amount of overlap between predators' foraging areas. The degree of overlap in foraging areas shapes species interactions, and as the overlap between species increases, we see decreasing benefits from species-rich communities. In contrast, diversity in body mass only improves prey suppression when there is significant variation in temperature.

Key words: biodiversity; body size; foraging area; intraguild interactions; mathematical modeling; optimization; predator–prey interactions; prey suppression; species traits; temperature dependence.

Received 11 May 2020; accepted 20 May 2020. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2020 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

³Present address: Department of Mathematics & Statistics, Texas Tech University, Lubbock, Texas, USA.

† **E-mail:** btenhumberg2@unl.edu

INTRODUCTION

There is a long-standing debate on the value of biodiversity in agricultural ecosystems, often in the context of prey suppression as an ecosystem service (Bianchi et al. 2006, Geiger et al. 2010, Winqvist et al. 2011). In many cases, herbivore prey populations can be effectively suppressed by a small group of specialist predators, such as ladybird beetles feeding on aphids or predatory mites feeding on spider mites. When these specialists are not abundant, such as early in a growing season, herbivore populations may be suppressed by a community of generalist predators (Pekár et al. 2015, Athey et al. 2016). Since

generalist predators also consume other members of the predator community (intraguild predation), the benefit of a high number of predator species (predator diversity) is unclear. The outcome of prey suppression is determined by a range of possible intraguild (predator–predator) interactions. For example, two generalist predator species might engage in intraguild predation or interference competition. As predators spend more time attacking or competing with one another, the consumption of prey decreases (Sitvarin and Rypstra 2014). The number of possible interactions, and outcomes of those interactions, dramatically increases with the number of predator species (for an overview, see Tschamntke et al.

2007, Letourneau et al. 2009, Griffin et al. 2013). Furthermore, it is difficult to empirically address these questions in controlled microcosms, where interactions are complicated by higher encounter rates when compared to field conditions (Straub et al. 2008). In this work, we use a mathematical model to develop an understanding of how diversity in predator traits impacts interactions between a large number of species in order to predict the relationship between predator diversity and prey suppression.

It is commonly assumed that the magnitude of prey suppression depends on the diversity of predator traits represented in the predator community (Straub et al. 2008, Crowder and Jabbour 2014, Greenop et al. 2018, Perović et al. 2018). Relevant traits are behavioral or physiological characteristics of a species, such as a predator's foraging behavior or body mass. Body mass (W) determines suitable prey size, since a predator might not be able to hunt prey much larger than itself or efficiently consume prey much smaller than itself, with larger species generally consuming larger prey items than smaller species. In addition to determining its range of suitable prey sizes, body mass is related to a species' metabolism, activity levels, and death rates (Brown et al. 2004, Gilljam et al. 2011), which in turn affect intraguild interactions and prey suppression. For example, a large predator species has a high metabolic rate and activity level, which means it will rapidly traverse its environment and encounter other individuals with high frequency. The outcome of any encounter depends on the relative size difference between species, with larger species typically consuming smaller species. However, large predators' high metabolic demands increase the risk of starvation.

The trade-off between an individual's metabolic demands and activity levels determines its efficiency as a predator. Importantly, insect metabolic rates (x) are also affected by temperature (T) ($x = W^{c_1} e^{c_2 T}$ for constants c_1, c_2 ; Rall et al. 2010). Hence, in environments with rising temperatures, larger individuals are more likely to die of starvation than smaller individuals. We therefore expect that changing temperatures will influence the efficiency of predators, since the trade-off between individuals' metabolic demands and activity levels will cause larger predators to become inefficient at higher temperatures.

Because of this, we hypothesize that diversity in body mass will permit consistent and effective prey suppression in environments that may experience a large range of temperatures. In order to predict the effect of increasing temperatures and variability due to climate change on the benefits of biodiversity for prey suppression, we must understand the effect of body mass on predator-prey interactions. Mathematical models are a powerful tool for predicting predator-prey interaction strengths resulting from the complicated relationships between body mass and other species characteristics (Brose et al. 2006, Berlow et al. 2009, Boit et al. 2012).

Along with body mass, encounter rates between individuals are affected by species' foraging areas. We consider a foraging area to be the physical region a species traverses in search of resources. For example, an herbivorous prey species' foraging area might consist of its host plant. In order to consume the herbivore, a predator species' foraging area must overlap with the location of the prey species (e.g., plant leaves). Other species in the predator community may forage over different portions of their prey's habitat (e.g., plant stem). The degree to which two predator species' foraging areas overlap will determine the likelihood that predators encounter one another while foraging. A high degree of overlap permits increased levels of intraguild predation, while a low degree of overlap reduces competition for prey items. Foraging area therefore affects interactions between species (Schmitz 2007, Straub and Snyder 2008), and empirical results indicate that this can affect intraguild interactions and prey suppression (Woodcock and Heard 2011). We expect that diversity in foraging area and a low degree of overlap will improve prey suppression.

In this manuscript, we present a generalizable, allometric model to investigate the benefit of high generalist predator diversity on suppressing herbivorous pest species in the absence of specialist predators. Populations of small herbivores, such as aphids or spider mites, increase rapidly during a growing season. Generalist predators often have a much longer generation time and consume a range of different prey species during their lifetime. This means that predator reproduction is decoupled from the consumption of a single prey species. In contrast, predator

mortality and the degree of herbivore suppression are affected by intraguild interactions. We utilize a model for these interactions which incorporates temperature-dependent trade-offs between mobility and metabolic rates and scales encounter rates according to overlap in predator foraging areas. We apply our model to a specific community of terrestrial arthropods in an agricultural field and simulate the prey suppression outcomes caused by a range of distributions in body size and foraging area in the predator community. Using an optimization approach, we identify predator communities which minimize the predicted average pest population size. The utility of this approach is that we can disentangle the interactions and traits which cause similar outcomes in true ecosystems.

Using our theoretical model, we identify the conditions under which intraguild predation and interference reduce the efficiency of diverse predator communities as well as the types of diversity which improve prey suppression. We predicted that diversity in predator body mass and foraging area would both improve prey suppression. We also predicted that increased temperatures would lead to optimal communities comprised of smaller predators. Although diversity in foraging area had a strong effect on optimal communities, we find that diversity in body mass was less important than expected. We discuss these results and identify areas where additional empirical information will improve theoretical predictions of prey suppression.

METHODS

Mathematical model for predator–prey dynamics

We expand the model from Schneider et al. (2012), which describes intraguild interactions (intraspecific competition and intraguild predation) such that body mass determines encounter rates, feeding preferences, and metabolic constraints. We scale encounter rates according to overlap in foraging area and incorporate intraguild interference, as described in Laubmeier et al. (2018). The resulting model can be applied to communities of varying size or trophic complexity, but must be restricted to generalist, ectothermic predators which reproduce on a longer timescale than their herbivore prey. We

model the population density $N(t)$ of the herbivore and $M_i(t)$ of predator species i at time t in the range $0 < t < t_f$, where t_f is necessarily less than the reproductive time of the predator species. We consider the case with s species such that $i = 1, 2, \dots, s$ and denote the prey with index $i = 1$ and predators with indices $i = 2, 3, \dots, s$. The dynamics for population densities are given by.

$$\begin{aligned} \frac{dN}{dt} &= \left[r - \sum_{j=2}^s \frac{a_{1j}v_{1j}M_j}{F_j} \right] N \text{ for the herbivore prey species,} \\ \frac{dM_i}{dt} &= \left[-x_i - \sum_{j=2}^s \frac{a_{ij}v_{ij}M_j}{F_j} \right] M_i \text{ for predators species } i=2,3,\dots,s, \\ F_j &= 1 + c_jM_j + a_{1j}v_{1j}h_{1j}N + \sum_{i=2}^s a_{ij}v_{ij}h_{ij}M_i + \sum_{m \neq i, m=2}^s b_0 a_{im}v_{im}M_m, \end{aligned} \tag{1}$$

where j, l , and m are species indices with the same meaning as i . We describe the terms in the differential equations below and summarize the biological meaning of model parameters in Table 1.

The growth rate for the herbivore prey population is a constant, positive value (r) that accounts for intrinsic birth and death processes. The herbivore prey population also decreases due to predation, which occurs at the rate $a_{1j}v_{1j}M_j/F_j$ for every potential predator species j . Predator populations decline due to metabolic death rates (x_i) and suffer losses due to intraguild predation, following the same relationship as in the herbivore prey population.

Individuals of species i utilize the same foraging area of individuals of species j with probability ν_{ij} . When the foraging areas of two species

Table 1. Biological interpretation of model quantities in (1).

Quantity	Biological interpretation
N	Population density of herbivore prey
M_i	Population density of predator i
F_j	Functional response for predator species j
r	Population growth rate for herbivore prey
x_i	Population death rate for species i
a_{ij}	Per-capita attack rate of species i on species j
ν_{ij}	Foraging similarity between species i and species j
c_j	Per-capita intraspecific competition rate for species j
h_{ij}	Time required for species j to handle prey of species i
b_0	Time required for non-consumptive intraguild interactions

overlap, they can encounter one another, and an attack on species i by species j occurs at rate a_{ij} . However, the amount of time that predators of species j can spend hunting is limited by the time spent on other activities and is quantified by the “functional response” (Skalski and Gilliam 2001) for species j (F_j). These other activities include the time a predator spends engaging in intraspecific competition ($c_j M_j$), hunting and digesting herbivore prey ($a_{1j} \nu_{1j} h_{1j} N$), hunting and digesting alternative prey items from other predators of species l ($a_{lj} \nu_{lj} h_{lj} M_l$), and evading intraguild interference from predators of species m ($b_{0j} a_{jm} \nu_{jm} M_m$). Intraguild interference may overlap with intraspecific competition in cannibalistic species, and so we require that . Foraging area overlap, quantified by ν_{ij} , impacts the rate at which intraguild predation and interference occur.

We replace model parameters with descriptions of how body mass affects the mechanisms driving predator interactions. Attack rates are given by.

$$a_{ij} = a_0 W_i^{1/4} W_j^{1/4} \left(\frac{W_j/W_i}{R_j} e^{1 - \frac{W_j/W_i}{R_j}} \right)^\phi, \quad (2)$$

where W_i is the average mass of an individual of species i and a_0 , R_j , and ϕ are constants. We assume that a species’ speed increases with its body mass. The speed of a species is proportional to $W_i^{1/4}$ and the speed of two individuals determines the rate at which they encounter and attack one another. The attack rate between species i and species j is therefore.

$$a_0 W_i^{1/4} W_j^{1/4}$$

where a_0 is a normalizing constant which scales the relationship between species speeds and attempted attacks. However, not every encounter between a predator and potential prey results in a predation event. The probability of a successful attack by species j on species i depends on the relative sizes of both species (W_j/W_i). There is an ideal predator–prey body mass ratio (R_j) at which species j is always successful in attacking its prey. If the true predator–prey body mass ratio (W_j/W_i) is close to this value, there is a high probability for species j to successfully attack species i . The probability of a successful attack by species j on species i is therefore given by.

$$\left(\frac{W_j/W_i}{R_j} e^{1 - \frac{W_j/W_i}{R_j}} \right)^\phi,$$

where ϕ is a tuning parameter. When $\phi=0$, attack rates are not affected by predator–prey body mass ratios. Encounters between individuals of the same species might result in intraspecific competition for resources. We therefore specify the rate of intraspecific competition as.

$$c_j = c_0 W_j^{1/4} W_j^{1/4} = c_0 W_j^{1/2},$$

where c_0 is a scaling constant for the rate at which competition occurs.

We assume that the amount of time a predator of species j handles a prey item of species i depends on the relative sizes of both species (W_i/W_j) because predators require more time to consume relatively large prey. The time required for an individual of species j to handle a prey item of species i is.

$$h_{ij} = h_0 (W_i/W_j)^{1/4},$$

where h_0 quantifies the proportional increase in handling time with increasing body mass ratio. Metabolic rates, and hence predator penalties, increase with temperature and body mass. The metabolic death rate for the predator population of species i is.

$$x_i = x_0 W_i^{3/4} e^{-E/kT},$$

where x_0 is a scaling constant for the penalty, E is activation energy, k is the Boltzmann constant, and T is the ambient temperature. We summarize the biological meaning of model parameters in Table 2 and refer to Schneider et al. (2012) and references therein for a more detailed description of the meaning and units of measurement for body mass-dependent parameters (a_{ij} , c_j , h_{ij} , x_i).

Optimizing predator communities

In order to identify how diversity in predator body mass or foraging area impacts prey suppression, we seek predator communities which minimize the average prey population density over n time steps. The average population density is given by

Table 2. Biological interpretation of quantities in model parameterization.

Quantity	Biological interpretation
W_i	Average body mass for individuals of species i
a_0	Scaling constant for encounter rates
R_j	Ideal predator-prey body mass ratio for species j
ϕ	Sensitivity of attack success to predator-prey body mass ratio
c_0	Scaling constant for intraspecific competition
h_0	Scaling constant for handling time
x_0	Scaling constant for metabolic death rates
E	Activation energy
k	Boltzmann's constant
T	Ambient temperature (in Kelvin)

$$C = \frac{1}{n} [N(t_1) + N(t_2) + \dots + N(t_n)]$$

where $N(t_d)$ denotes the prey population density at time t_d prior to the reproductive time of the predator species, for $d = 1, 2, \dots, n$ and $0 < t_1 < t_2 < \dots < t_f$. For a given prey population with initial density $N(0)$, we begin by specifying a set of predator species j typically associated with the prey species. Each predator species j has average body mass W_j , a specific foraging area, and feeding interactions with other species. For each set of initial predator densities $M_2^0, M_3^0, \dots, M_s^0$, which we denote by $\{M_j(0)\}$, we simulate the population dynamics from (1) to obtain the prey population $N(t)$ for n time steps. The average prey population for these initial predator densities is.

$$C(\{M_j(0)\}) = \frac{1}{n} [N(t_1; \{M_j(0)\}) + \dots + N(t_n; \{M_j(0)\})],$$

where we use the notation $N(t; \{M_j(0)\})$ to emphasize that solutions to $N(t)$ are dependent on initial predator densities $\{M_j(0)\}$.

We obtain the optimal predator community for prey suppression by minimizing $C(\{M_j(0)\})$ over all possible initial densities of all predator species. We assume that there is not an unlimited supply of predators and require that.

$$\sum_{j=2}^s M_j(0) = M^* \quad (3)$$

for a constant number M^* determined by the biology of the system. In the absence of this type of constraint, we would have the unrealistic

outcome that predator communities could always include more predators, which would lower the number of prey indefinitely without ever attaining a minimum solution. We note that depending on the study system, an inequality constraint ($\sum M_j(0) \leq M^*$) or different constraining values, such as the biomass or management cost of a predator community, could be substituted here.

Our optimization problem is therefore to choose $\{M_j(0)\}$ to minimize $C(\{M_j(0)\})$, subject to model dynamics (1) and the constraint (3). We refer to the Appendix S1 for a mathematical proof regarding the existence of solutions to this optimization problem. In practice, we solve the problem with the MATLAB function `fmincon`, which numerically minimizes a cost function according to specified constraints (for more details, see Appendix S2 or code at DOI:10.5281/zenodo.4093174). However, this minimization might be sensitive to where it begins searching for a solution. We therefore employ the multi-start function, which repeats the minimization over different starting points. This guards against the possibility of non-unique (locally minimizing) solutions, where the solution found by `fmincon` depends on the starting point of the search.

A case study: terrestrial arthropods

We illustrate the effect of body mass and foraging area on optimal predator communities for prey suppression through a specific example. Because a previous study provided us with empirical estimates for many model quantities, we consider the suppression of the bird cherry-oat aphid, *Rhopalosiphum padi*, feeding on barley host plants in a spring field season. Aphids are widespread pests and frequently the subject of biological control studies (Brodeur and Rosenheim 2000, Snyder and Ives 2003). Additionally, *R. padi* are parthenogenetic and capable of telescoping generations, resulting in rapid reproduction (Villanuevab and Strong 1964) which occurs over shorter timescales than the generalist predators in this system. For details on the lifecycles and biology of *R. padi*, we refer to Dixon (1971) and Leather and Dixon (1981). This aphid species is prey to a generalist community of spiders and groundbeetles, which also engage in complex intraguild interactions (Hodge 1999, Lang 2003).

Averaging over population density (M_j) and body mass (W_j) data from Curtsdotter et al. (2019), we consider the community of predators depicted in Fig. 1.

This predator community is comprised of five differently sized groundbeetle species and four spider species with less variation in body mass than in the groundbeetle species. We use the population density data to specify the constraint (3) for the optimization problem. That is, letting $\{M_j\}$ be the densities of the predator community reported in Fig. 1, we have $M^* = \Sigma M_j$ the total initial predator population density. We use the average start-of-season aphid populations in Curtsdotter et al. (2019) as the initial aphid population density. In addition to the aphid prey, predators can potentially consume every other predator species in the community, including members of their own species. We note that groundbeetles generally forage on the ground, possibly burrowing into the dirt or reaching up the base of a plant. Some species of spider actively forage on the ground or climb up plants (*Tetragnathidae*, *Lycosidae*), while others form webs to catch prey (*Linyphiidae*). However, we did not have specific measurements or observations of predator foraging area in this community. We therefore investigate the effect of different assumed overlaps in foraging area (ν_{ij}) on optimal predator communities, since foraging area is an important aspect of our model.

We obtain estimates of a_0 , ϕ , h_0 , and r_1 from Wootton et al. (2020) E and x_0 from Schneider et al. (2012). We consider temperatures in the range of $T = 15^\circ\text{C}$ to $T = 45^\circ\text{C}$, which is consistent with temperatures observed in the field (Curtsdotter et al. 2019). The predators' preferred predator-prey body mass ratios (R_j) are difficult to measure and have minor effects on optimization outcomes. We therefore set these values such that every predator has a 100% success rate when consuming aphids. In doing so, we focus our investigation on the effect of predator body mass diversity on prey suppression, instead of on optimal predator-prey body mass ratios. Based on aphid population dynamics described in Curtsdotter et al. (2019), we restrict our simulations and optimization to a 30-d period. Over this period of time, aphid populations colonized barley fields and increased until reaching a peak density. After this, populations declined rapidly. The declines did not always line up with a decline in crop quality, and possible explanations include microclimate changes or avian predators.

We found a range of estimates in the literature for c_0 (between 0.12 and 1.09, Schneider et al. 2012, Jonsson et al. 2018), which is related to intraspecific competition between predators, and we only had one estimate of b_0 (Wootton et al. 2020), which is related to intraguild interference between predators. We explored c_0 values between 0 (no intraspecific competition) and 1

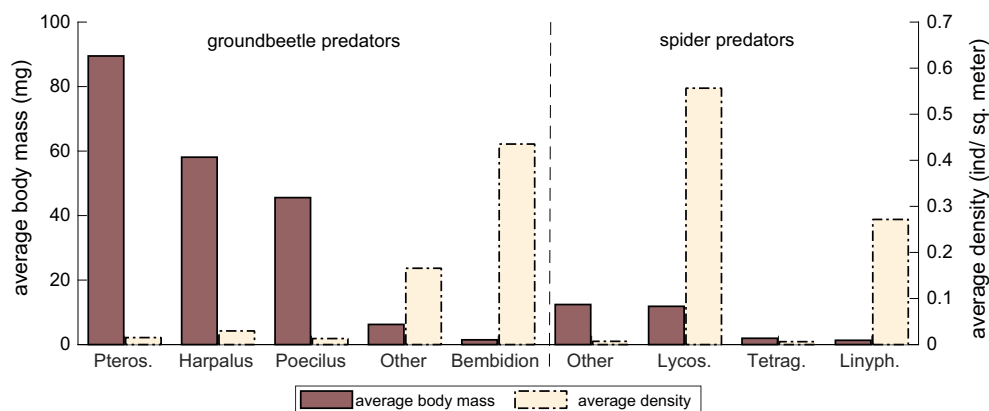


Fig. 1. The average body mass (left axis, solid bars) and average population density (right axis, dotted bars) of predator species in our study system. The dashed line indicates the break between groundbeetle groups (*Pterostichus*, *Harpalus*, *Poecilus*, "Other Carabid," and *Bembidion*) and spider groups ("Other Spider," *Lycosidae*, *Tetragnathidae*, and *Linyphiidae*). The groups "Other Carabid" and "Other Spider" are made up of rare species not included in the previous groundbeetle and spider categories.

(high levels of intraspecific competition) and b_0 values from 0 (no intraguild interference) to 10 (high levels of intraguild interference). In the example predator community (Fig. 1), the average effect of intraguild interference on prey suppression when $b_0 = 10$ matches the effect of intraspecific competition on prey suppression when $c_0 = 1$. We list the values for model parameters and quantiles from Fig. 1 in the Appendix S3.

RESULTS

Effects of foraging area on optimal community composition

We first investigate the effect of predator foraging area on prey suppression efficiency in predator communities. We consider three cases for how predator foraging area might overlap: (1) Every predator forages in the same area, (2) there are two foraging areas, which overlap completely for predators in the same group (“groundbeetle” and “spider”), but only slightly with predators from the other group, and (3) every predator species has its own foraging area, which overlaps moderately with predators in the same group (“groundbeetle” or “spider”) and slightly with predators from the other group. Within each predator species, foraging areas overlap completely, and predators encounter members of other species according to the degree of overlap between foraging areas. See Fig. 2 for a diagram of the different overlap scenarios. In all three cases, we solve the optimization problem over a range of ambient temperatures, assuming that average temperatures vary between seasons but are constant within a single 30-d simulation period.

When all predators share a single foraging area (Fig. 3a), the optimal predator community for each temperature is always comprised of a single-predator species. Temperature affects metabolic penalties (x_i), which causes optimal predator species to change from large species at lower temperatures to small species at higher temperatures. When foraging area overlaps for predator species in the same group (Fig. 3b), spiders are more likely to encounter other spiders than they are to encounter groundbeetles, and vice versa. In this case, the optimal predator community for a single temperature is always

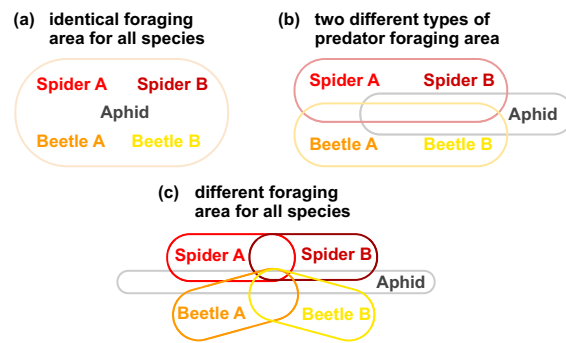


Fig. 2. Diagram of overlap in predator foraging areas in a simplified scenario, demonstrating (a) one foraging area, (b) two foraging areas, and (c) four foraging areas. The example uses one prey (Aphid) and four predators (Spider A, Spider B, Beetle A, and Beetle B). These could correspond, for example, to Lycosidae, Tetragnathidae, Harpalus, and Poecilus in the true community.

comprised of one spider and one groundbeetle species, and the optimal species from either group changes with temperature. When each predator species has its own foraging area (Fig. 3c), multiple spider and groundbeetle species form an optimal predator community for a single temperature. Again, the composition of predator species that is best in suppressing prey populations varies with temperature. This change can occur gradually with changing temperature or suddenly; for example, the densities of *Pterostichus*, *Harpalus*, and *Poecilus* change gradually in optimal predator communities for temperatures ranging between 15°C and 25°C, but *Poecilus* is almost half of the optimal predator community at 29°C before “Other Carabid” suddenly replaces *Poecilus* at 30°C. For most of the remaining results, we focus on scenarios where every predator species has its own foraging area (as in Fig. 3c) because this is a necessary condition for high biodiversity to improve prey suppression.

Optimal predator communities under varied temperatures

First, we consider how sensitive the optimal predator community with diverse foraging area is to changes in temperature between years (Fig. 4). We focus our comparison on three single-species communities representing a range of body masses: *Poecilus* (a large predator), the

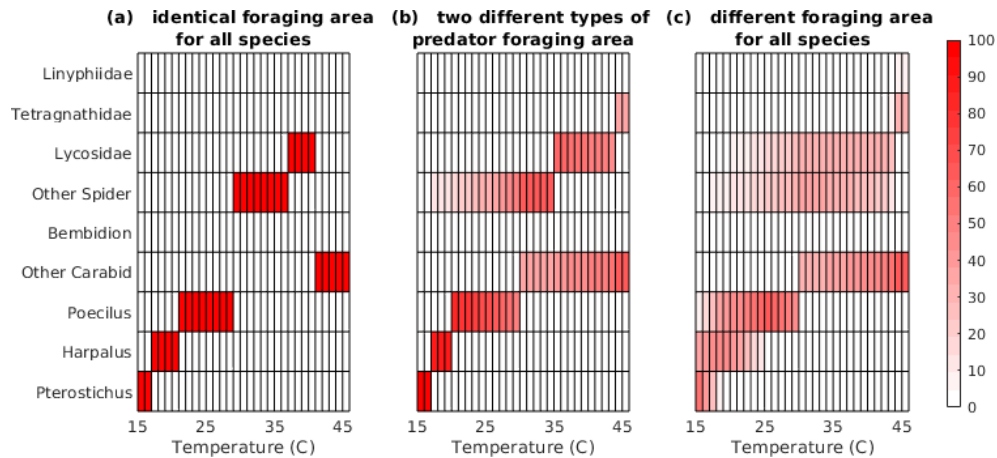


Fig. 3. Composition of initial densities in the optimal predator community over a range of temperatures, for (a) one foraging area, (b) two foraging areas, and (c) nine foraging areas. The horizontal dashed line indicates the break between spider and groundbeetle predators.

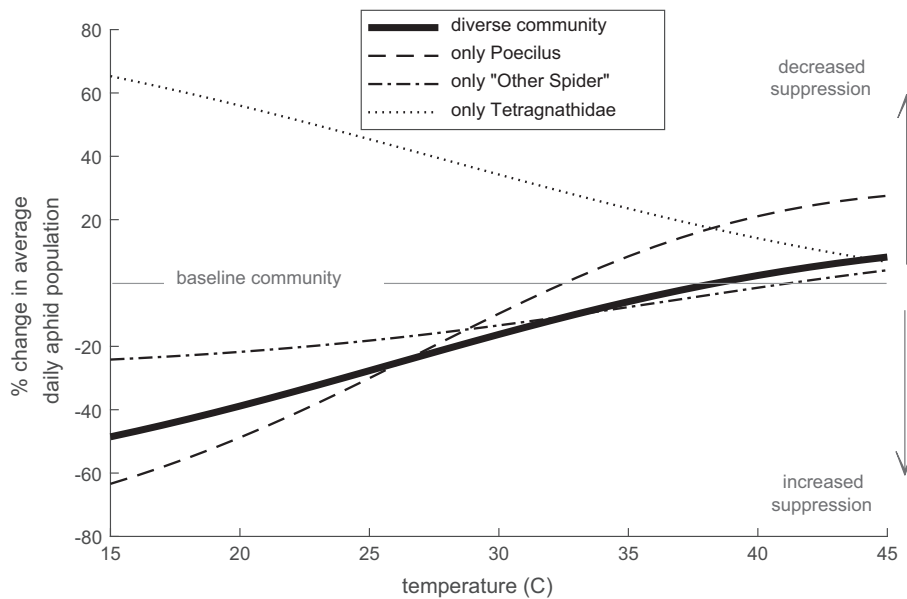


Fig. 4. Percent change in average daily aphid population for temperatures between $T = 15^{\circ}\text{C}$ and $T = 45^{\circ}\text{C}$. The horizontal line indicates comparison to the baseline predator community (Fig. 1). Single-predator communities are indicated by thin, dashed lines, and a multi-predator community is indicated with a thick, solid line. Foraging area is as in Fig. 3c.

group “Other Spider” (a medium-sized predator), and *Tetragnathidae* (a small predator). These predator species suppressed prey populations the most over the full temperature range, compared to species in the same size categories. In our comparison, we also include the predator

composition found in the field from Fig. 1 (“baseline community”) and a “diverse community” where the initial density of each predator species is the species’ average initial density over all optimal predator communities in Fig. 3c. Compared to the “baseline community,” the

“diverse community” results in a 14.6% decrease in the prey population when averaged over temperatures between 15°C and 45°C (Fig. 4). No single-species community matches this performance; *Poecilus* decreases the average prey population by 7.6%, the group “Other Spider” decreases the average prey population by 10.4%, and *Tetragnathidae* increases the average prey population by 31.6% over the same range of temperatures. As we found previously, larger predators improve prey suppression at lower temperatures, while smaller predators improve prey suppression at high temperatures.

Next, we investigate the effect of temperature variation within a growing season. We use temperature recordings from 9 field sites in Curtsdotter et al. 2019, which had mean 20.2°C and median 17.7°C. We preserve autocorrelation in the data by taking every possible 3-day window of temperatures. We conduct 5000 simulations with 30-d temperature fluctuations randomly drawn from these windows and calculate the average daily prey population. We

compare single-predator communities to the true community and two communities comprised of optimal predators from Fig. 3. The initial distribution of optimal predators is determined by relative abundances in the true community or by weighting predators according to the frequency of true temperatures at which they are optimal (see Fig. 5). We find that without diversity in foraging area (Fig. 6a), single-species communities comprised of the most efficient beetles (*Harpalus* and *Poecilus*) outperform diverse communities. When predators utilize different foraging areas (Fig. 6b), the diverse communities using optimal predators attain slightly lower levels of prey suppression and, more importantly, reduce variation in prey suppression across simulations.

Interplay between intraguild interactions and diversity

We next explore the effect of different combinations of intraspecific competition (scaled by the parameter c_0) and intraguild interference

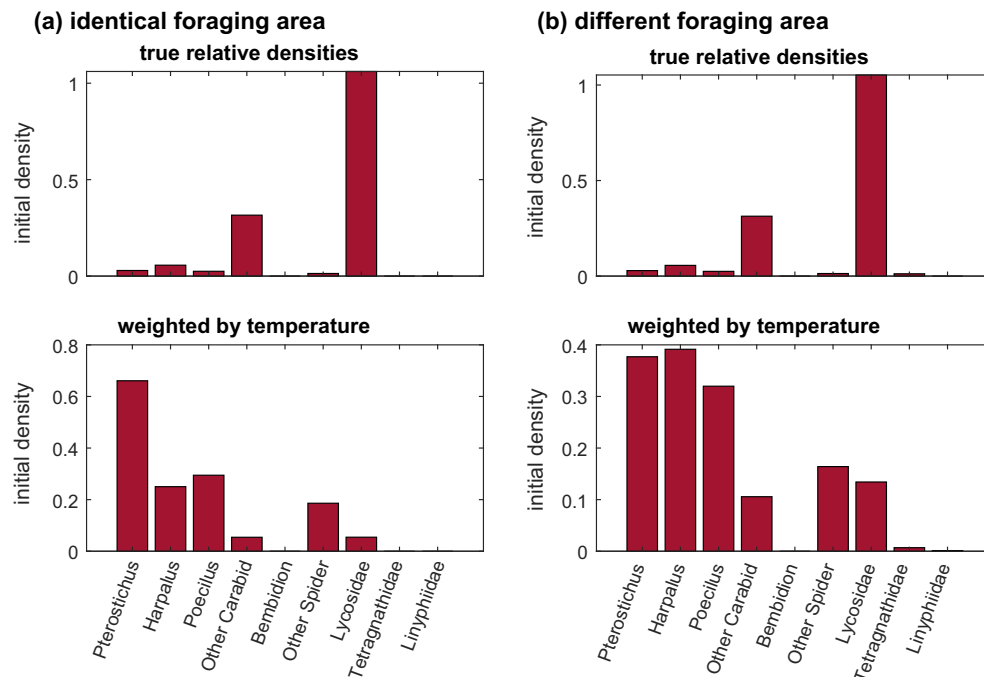


Fig. 5. Composition of predator communities for comparison in Fig. 6. Communities utilize optimal predators identified in Fig. 3a (left) or Fig. 3c (right). Initial densities are determined according to true relative densities from the field (top) or weighted by the frequency of corresponding optimal temperatures over one season in the field (bottom).

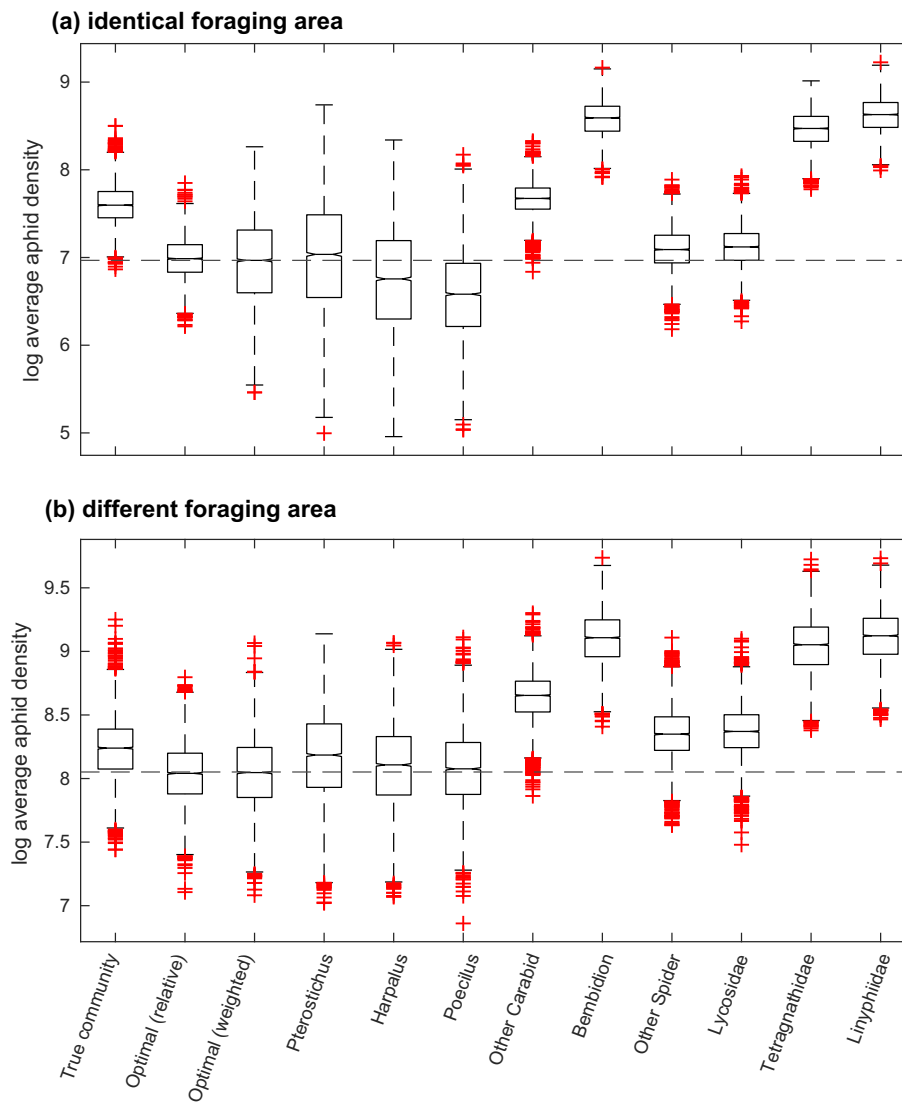


Fig. 6. Aphid density under single-predator and diverse communities with time-varying temperature. Daily temperatures were drawn from field data, and simulations were repeated over 5,000 random draws from daily temperatures. Foraging area is as in Fig. 3a (top) or Fig. 3c (bottom).

(scaled by the parameter b_0) on optimal predator communities. For each pair of b_0 and c_0 values, we find the optimal predator community for temperatures ranging between 15°C and 45°C and foraging area overlap as in Fig. 3c. We count the number of species in each optimal predator community and report the average number of predator species over all temperatures in Fig. 7. We find that the optimal number of predator species increases with increasing levels of

intraspecific competition and decreases with increasing levels of intraguild interference. The value of c_0 determines how strongly predators' attack rates decrease due to competition within a predator species. As c_0 increases, the number of species in the optimal predator community increases (vertical slices of the contour diagram in Fig. 7). Regardless of how many species are present, the optimizing constraint (3) requires that every optimal predator community be

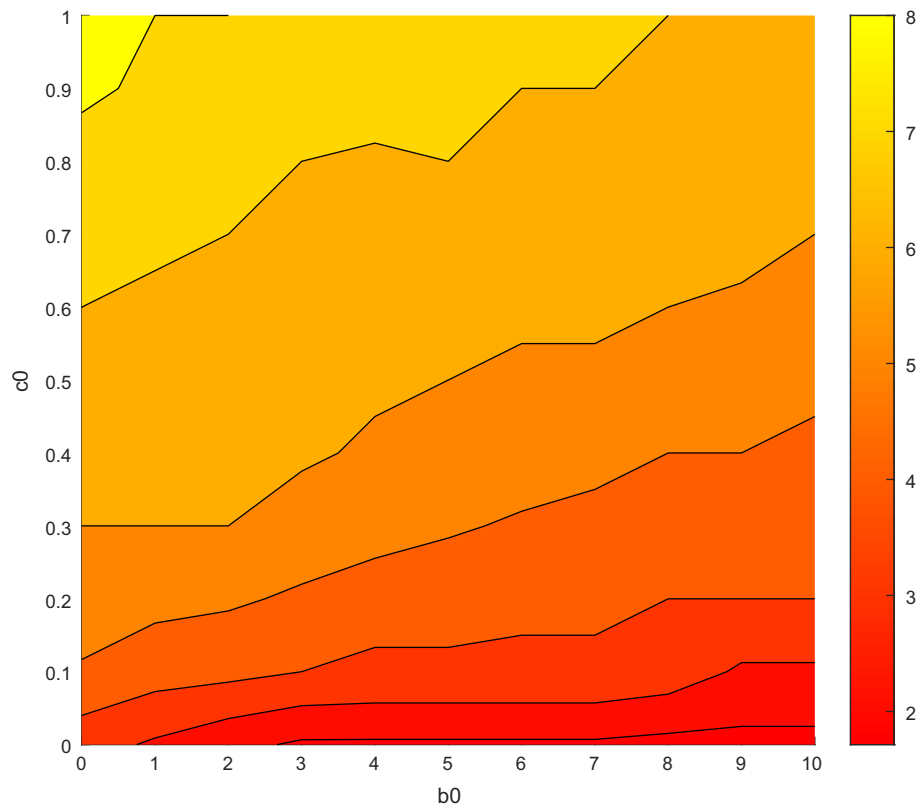


Fig. 7. Average number of species in optimal predator communities for varying levels of intraguild interference (b_0) and intraspecific competition (c_0). Averages are taken over temperatures between $T = 15^\circ\text{C}$ and $T = 45^\circ\text{C}$. Foraging area is as in Fig. 3c.

initially comprised of the same number of individuals; each population in a community of many species must have lower initial densities than each population in a community of fewer species. Communities with many predator species minimize the effect of intraspecific competition by reducing the number of individuals within each species. The value of b_0 determines how strongly predators' attack rates decrease due to interference from predators in other species. As b_0 increases, the number of species in the optimal predator community decreases (horizontal slices of the contour diagram in Fig. 7). In comparison with c_0 , changes in b_0 have a small effect on the average number of predators in the optimal community. The relative magnitude of these two parameters (and therefore the cost of intraspecific competition compared to intraguild interference) determines the number of species in an optimal community.

DISCUSSION

There is substantial ecological interest in understanding the relationship between the control of insect pests and biodiversity in natural enemy guilds. Reducing species richness (number of species) (Hooper et al. 2005, Cardinale et al. 2006) and evenness (skewed relative abundance distributions) (Hillebrand et al. 2008, Crowder et al. 2010) can weaken or improve biological control. However, our understanding of these outcomes' underlying mechanisms is limited (Crowder and Jabbour 2014). Our model suggests that overlap in foraging area within predator communities is key to predicting the effect of biodiversity on prey suppression (Fig. 3a–c). If predator species forage in overlapping areas, predators are more likely to encounter one another while hunting for prey. This results in frequent occurrences of intraguild predation and interference, which reduces prey suppression. In the case of largely

overlapping foraging areas, optimal communities for prey suppression are comprised of a single-predator species, for a given temperature. These results align with multiple observations that functional diversity positively impacts prey suppression (Greenop et al. 2018). However, temperature determines which species is the most efficient predator, and so in environments with significant temperature fluctuation between years, predator biodiversity is beneficial regardless of foraging area overlap.

Diversity in foraging area improves prey suppression

In Fig. 3, we find that it is an advantage for optimal predator communities to be comprised of multiple predator species which forage in different areas. This is in line with empirical studies, which have shown that prey suppression is often improved in complex habitats where foraging behavior is likely more variable (Finke and Denno 2006) and when predators exhibit different patterns of habitat use or hunting behaviors (Woodcock and Heard 2011). The importance of foraging area overlap to prey suppression is also demonstrated by Northfield et al. (2017) spatial using a three species model (two predators, one prey). We expand this by increasing the number of possible predators, all of which are characterized by a combination of traits representative of a real community (Fig. 1), as well as considering non-fatal and non-consumptive effects of intraguild interference and interactions with temperature. In our model, predator interactions depend on foraging area overlap, but predator success is also determined by the fundamental trade-off between body size, prey size preferences, and temperature. Studying predator traits in isolation does not necessarily lead to meaningful predictions of prey suppression. Prey suppression by a predator community might be more or less effective than predicted when different traits interact in unexpected ways.

Empirical studies of intraguild predation and its effect on prey suppression (Rosenheim et al. 1993) suggest that the presence of very small predator species may impair prey suppression by very large predator species. Our model provides an explanation for this observation when comparing optimal predator communities at different temperatures (Fig. 3c). When one predator completely replaces another in the optimal community, it shows that neither predator can be effective alongside the other, due to intraguild

interference or predation. For instance, at 29°C the optimal predator community includes the relatively large species *Poecilus* without the relatively small group “Other Carabid.” However, a one degree increase in temperature causes *Poecilus* to be replaced by “Other Carabid” in the optimal predator community. *Poecilus* represents a highly mobile predator that consumes individuals much smaller than itself, which would impose a large predation pressure on “Other Carabid” if both species were present in the community. In contrast, other optimal predator communities included *Poecilus* alongside large groundbeetles (*Pterostichus* and *Harpalus*, similar foraging area) or small spiders (“Other Spider” and *Lycosidae*, dissimilar foraging area). Taken together, these modeling results illustrate how the interplay between diversity in body mass and diversity in foraging area can lead to positive or negative prey suppression outcomes. Specifically, we see that high diversity in body mass paired with overlapping foraging areas can impede prey suppression.

Body mass diversity is sometimes beneficial

When predators do not utilize different foraging areas (Fig. 3a), diversity in predator body mass is only beneficial if there is large annual variation in average temperature. At low temperatures, large predators (*Pterostichus*, *Harpalus*, and *Poecilus*) are most effective, since they are highly mobile and encounter prey more frequently than small predators. As temperatures increase, these same predators are ineffective because metabolic rates increase more quickly with temperature for large predators than small predators. If temperatures vary between years, the optimal predator community for prey suppression therefore might include small and large species which are highly efficient in controlling the prey population for any temperature in a given year. These expectations align with the insurance hypothesis that increasing biodiversity insures ecosystems against declines in their functioning caused by environmental fluctuations (Naeem and Li 1997, Yachi and Loreau 1999). In the context of this hypothesis, temperature is the environmental driver fluctuating between years and prey suppression is a type of ecosystem function which depends on how species in the predator community respond to temperature.

In Fig. 4, we explore the conditions under which the insurance against temperature variability between years can outweigh the penalties of a

suboptimal predator community, when combined with diversity in foraging area. We find that there is a small range of temperatures (~26–32°C) where the “diverse community” identified by our optimization procedure outperforms communities comprised of only small or large predators. Outside this range, the net benefit attained by the diverse community depends on the distribution of temperatures between years. However, averaging across the range of temperatures considered, the positive effects of diversity in body mass outweigh the negative effects of intraguild interference and predation associated with a larger number of species. For instance, large groundbeetles effectively suppress the prey population at low temperatures, but they are ineffective at higher temperatures. The difference in performance between large groundbeetles and the diverse community is larger at high temperatures (when the diverse community is more effective) than at lower temperatures (when large groundbeetles are more effective).

In Fig. 6, we investigate whether insurance against temperature variation within a single year can demonstrate a benefit to diversity in body mass. We find that without diversity in foraging area, single-predator communities consistently attain the lowest level of prey suppression. The optimal predators at the mean or median of the season’s temperatures (large beetles *Harpalus* and *Poecilus*) outperform diverse communities. We again see that when predators utilize different foraging areas, the diverse communities outperform single-predator communities. Despite different distributions of initial predator abundances (comprised mainly of small spiders or large beetles), the two optimal communities we consider attain similar levels of prey suppression, and the inclusion of smaller predators in these communities results in smaller variation in prey suppression across different simulations (years). This provides some support for the insurance hypothesis, but at field-realistic temperatures, we cannot demonstrate a benefit to prey suppression which arises from only diversity in body mass (foraging areas must overlap).

Frequency of intraguild interactions drives diversity effects

Predator body mass and foraging area overlap are key characteristics of optimal predator communities largely because they determine the

frequency of intraguild interactions, such as intraguild interference and intraspecific competition. However, quantifying the significance of these interactions and their effects on prey suppression in the field presents a challenge. In our model, intraguild interference and intraspecific competition are controlled by the parameters b_0 and c_0 , respectively. We find that when intraspecific competition dominates (large values of c_0), prey suppression improves with increasingly diverse predator communities (Fig. 7). This is a by-product of reducing the number of competing individuals within predator groups and is not directly related to variation in predator body mass or foraging area. Although larger groundbeetles are more mobile and engage in intraspecific competition more frequently, foraging area does not interact with intraspecific competition at all because intraspecific foraging area is identical. In contrast, when intraguild interference dominates (large values of b_0), smaller groundbeetles and spiders face higher intraguild interference from larger predators. Decreasing the overlap in predator foraging areas can reduce this effect. Our model indicates that the effect of predator diversity on prey suppression depends on the balance of intraspecific competition and intraguild interference within predator guilds. Hence, modeling intraspecific competition without considering general intraguild interference may inflate the predicted value of predator richness by underestimating negative intraguild interactions. Similarly, models which do not include intraspecific competition may underestimate the positive effects of diversity on prey suppression.

Key takeaways for prey suppression

In summary, our results further the understanding of when, and under which conditions, increased biodiversity improves prey suppression in real ecosystems. We find that the most important factor for determining prey suppression is overlap in predator foraging area. Overlap in foraging area is, to a large degree, influenced by the underlying landscape in which predators interact. For instance, complex environments are more likely to foster diversity in foraging areas. This suggests that farmers may improve pest control by maintaining weedy crop margins, growing two or more crops in proximity (intercropping) (Zhang et al. 2017), or planting cover crops (Bryant et al. 2013). When negative

predator–predator interactions are mediated by diversity in foraging area, body mass diversity (even within a community of “suboptimal” predators) can improve resilience and overall prey suppression of a community when temperatures vary between years. However, if an environment does not permit diversity in foraging area, then low-diversity communities will be optimal. In this case, managers should identify the most efficient predators for their field conditions and augment predator communities with these species to improve prey suppression. The predators we identify as optimal are specific to our study system, but similar methods could be employed to identify optimal predators in other systems.

LITERATURE CITED

- Athey, K. J., J. Dreyer, K. A. Kowles, H. J. Penn, M. I. Sitvarin, and J. D. Harwood. 2016. Spring forward: molecular detection of early season predation in agroecosystems. *Food Webs* 9:25–31.
- Berlow, E. L., J. A. Dunne, N. D. Martinez, P. B. Stark, R. J. Williams, and U. Brose. 2009. Simple prediction of interaction strengths in complex food webs. *Proceedings of the National Academy of Sciences* 106:187–191.
- Bianchi, F. J., C. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proceedings of the Royal Society B: Biological Sciences* 273:1715–1727.
- Boit, A., N. D. Martinez, R. J. Williams, and U. Gaedke. 2012. Mechanistic theory and modelling of complex food-web dynamics in lake conformance. *Ecology Letters* 15:594–602.
- Brodeur, J., and J. A. Rosenheim. 2000. Intraguild interactions in aphid parasitoids. *Entomologia Experimentalis Et Applicata* 97:93–108.
- Brose, U., R. J. Williams, and N. D. Martinez. 2006. Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9:1228–1236.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Bryant, A., D. C. Brainard, E. R. Haramoto, and Z. Szendrei. 2013. Cover crop mulch and weed management influence arthropod communities in strip-tilled cabbage. *Environmental Entomology* 42:293–306.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989.
- Crowder, D. W., and R. Jabbour. 2014. Relationships between biodiversity and biological control in agroecosystems: current status and future challenges. *Biological Control* 75:8–17.
- Crowder, D. W., T. D. Northfield, M. R. Strand, and W. E. Snyder. 2010. Organic agriculture promotes evenness and natural pest control. *Nature* 466:109.
- Curtsdotter, A., H. T. Banks, J. E. Banks, M. Jonsson, T. Jonsson, A. N. Laubmeier, R. Bommarco. 2019. Ecosystem function in predator–prey food webs—confronting dynamic models with empirical data. *Journal of Animal Ecology* 88:196–210.
- Dixon, A. 1971. The life-cycle and host preferences of the bird cherry-oat aphid, *rhopalosiphum padi* L., and their bearing on the theories of host alternation in aphids. *Annals of Applied Biology* 68:135–147.
- Finke, D. L., and R. F. Denno. 2006. Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* 149:265–275.
- Geiger, F., et al. 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on european farmland. *Basic and Applied Ecology* 11:97–105.
- Gilljam, D., A. Thierry, F. K. Edwards, D. Figueroa, A. T. Ibbotson, J. I. Jones, R. B. Lauridsen, O. L. Petchey, G. Woodward, and B. Ebenman. 2011. Seeing double: size-based and taxonomic views of food web structure. *Advances in Ecological Research* 45:67–133.
- Greenop, A., B. A. Woodcock, A. Wilby, S. M. Cook, and R. F. Pywell. 2018. Functional diversity positively affects prey suppression by invertebrate predators: a meta-analysis. *Ecology* 99:1771–1782.
- Griffin, J. N., J. E. Byrnes, and B. J. Cardinale. 2013. Effects of predator richness on prey suppression: a meta-analysis. *Ecology* 94:2180–2187.
- Hillebrand, H., D. M. Bennett, and M. W. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520.
- Hodge, M. A. 1999. The implications of intraguild predation for the role of spiders in biological control. *Journal of Arachnology*, 27 351–362.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Jonsson, T., R. Kaartinen, M. Jonsson, and R. Bommarco. 2018. Predictive power of food web models based on body size decreases with trophic complexity. *Ecology Letters* 21:702–712.
- Lang, A. 2003. Intraguild interference and biocontrol effects of generalist predators in a winter wheat field. *Oecologia* 134:144–153.

- Laubmeier, A., K. Wootton, J. Banks, R. Bommarco, A. Curtsdotter, T. Jonsson, T. Roslin, and H. T. Banks. 2018. From theory to experimental design—quantifying a trait based theory of predator-prey dynamics. *PLOS ONE* 13:e0195919.
- Leather, S., and A. Dixon. 1981. Growth, survival and reproduction of the bird-cherry aphid, *rhopalosiphum padi*, on its primary host. *Annals of Applied Biology* 99:115–118.
- Letourneau, D. K., J. A. Jedlicka, S. G. Bothwell, and C. R. Moreno. 2009. Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* 40:573–592.
- Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. *Nature* 390:507.
- Northfield, T. D., B. T. Barton, and O. J. Schmitz. 2017. A spatial theory for emergent multiple predator–prey interactions in food webs. *Ecology and Evolution* 7:6935–6948.
- Pekár, S., R. Michalko, P. Loverre, E. Líznavá, and Ľ. Černecká. 2015. Biological control in winter: novel evidence for the importance of generalist predators. *Journal of Applied Ecology* 52:270–279.
- Perović, D. J., S. Gámez-Virués, D. A. Landis, F. Wäckers, G. M. Gurr, S. D. Wratten, M.-S. You, and N. Desneux. 2018. Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. *Biological Reviews* 93:306–321.
- Rall, B. C., O. Vucic-Pestic, R. B. Ehnes, M. Emmerson, and U. Brose. 2010. Temperature, predator–prey interaction strength and population stability. *Global Change Biology* 16:2145–2157.
- Rosenheim, J. A., L. R. Wilhoit, and C. A. Armer. 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia* 96:439–449.
- Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415–2426.
- Schneider, F. D., S. Scheu, and U. Brose. 2012. Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters* 15:436–443.
- Sitvarin, M. I., and A. L. Rypstra. 2014. The importance of intraguild predation in predicting emergent multiple predator effects. *Ecology* 95:2936–2945.
- Skalski, G. T., and J. F. Gilliam. 2001. Functional responses with predator interference: viable alternatives to the holling type ii model. *Ecology* 82:3083–3092.
- Snyder, W. E., and A. R. Ives. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology* 84:91–107.
- Straub, C. S., D. L. Finke, and W. E. Snyder. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control* 45:225–237.
- Straub, C. S., and W. E. Snyder. 2008. Increasing enemy biodiversity strengthens herbivore suppression on two plant species. *Ecology* 89:1605–1615.
- Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Reprint of “conservation biological control and enemy diversity on a landscape scale” [*biol. control* 43 (2007) 294–309]. *Biological Control* 45:238–253.
- Villanueva, J. R., and F. E. Strong. 1964. Laboratory studies on the biology of *rhopalosiphum padi* (homoptera: Aphididae). *Annals of the Entomological Society of America* 57:609–613.
- Winqvist, C., et al. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *Journal of Applied Ecology* 48:570–579.
- Woodcock, B. A., and M. S. Heard. 2011. Disentangling the effects of predator hunting mode and habitat domain on the top-down control of insect herbivores. *Journal of Animal Ecology* 80:495–503.
- Wootton, K., A. Laubmeier, A. Curtsdotter, T. Jonsson, R. Bommarco, H. Banks, and T. Roslin. 2020. From theory to experiment and back again — Challenges in quantifying a trait-based theory of predator-prey dynamics.
- Yachi, S., and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences* 96:1463–1468.
- Zhang, Z., C. Zhou, Y. Xu, X. Huang, L. Zhang, and W. Mu. 2017. Effects of intercropping tea with aromatic plants on population dynamics of arthropods in Chinese tea plantations. *Journal of Pest Science* 901:227–237.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3271/full>

Appendix S1: Existence of Optimal Predator Communities

We denote $\{M_i(t; NM_1^0, \dots, M_s^0)\}_{i=1}^s$ to be the solution, if it exists, of the initial value problem

$$\begin{cases} \frac{dM_i}{dt} = \left[r_i - x_i - \sum_{j \in \mathcal{C}_i} \frac{\tilde{a}_{ij}}{F_j} M_j \right] M_i, & i = 1, \dots, s \\ F_j = 1 + c_j M_j + \sum_{l \in \mathcal{R}_j} \tilde{a}_{lj} h_{lj} M_l + \sum_{m \in \mathcal{C}_j, m \neq j} b_0 \tilde{a}_{jm} M_m, & j = 2, \dots, s \\ M_i(0) = M_i^0, & i = 1, \dots, s \end{cases} \quad (1)$$

for constant values of $M_i^0 \geq 0$ over some interval $0 \leq t \leq t_f$. We note that this is a generalization of model (1), for $N = M_1$. The parameters r_i , x_i , \tilde{a}_{ij} , h_{ij} , and b_0 and population densities M_i are non-negative quantities. We seek to minimize

$$C(M_2^0, \dots, M_s^0) = \frac{1}{d} \left[M_1(t_1; \bar{M}_1^0, M_2^0, \dots, M_s^0) + \dots + M_1(t_d; \bar{M}_1^0, M_2^0, \dots, M_s^0) \right], \quad (2)$$

where $\bar{M}_1^0, t_1, \dots, t_d$ are fixed and inputs are subject to the constraint

$$\sum_{i=2}^s M_i^0 = M^*. \quad (3)$$

That is, the domain of $C(M_2^0, \dots, M_s^0)$ is the set

$$\mathcal{D} = \left\{ \{M_i^0\}_{i=2}^s \mid M_i^0 \geq 0 \text{ for } i = 2, \dots, s \text{ and } \sum_{i=2}^s M_i^0 = M^* \right\}.$$

We note that in some applications, it may be useful to implement an inequality constraint such that $\sum_{i=2}^s M_i^0 \leq M^*$; although we did not do so in this work, existence of solutions with an inequality constraint can be demonstrated using the same steps as below.

Since $M_i^0 \geq 0$, the constraint (3) implies that $0 \leq M_i^0 \leq M^*$ for all $i = 2, \dots, s$. Hence \mathcal{D} is closed and bounded. We therefore have that if $C(M_2^0, \dots, M_s^0)$ is continuous, the function attains its minimum over the domain, and at least one solution to the minimization problem exists.

We will use a special case of Theorem (7.1) from Coddington and Levinson (1955). The solution $\{M_i(t; M_1^0, \dots, M_s^0)\}_{i=1}^s$ is continuous in the s -dimensional domain of initial conditions if

$$f_i(M_1, M_2, \dots, M_s) = \left[r_i - x_i - \sum_{j \in \mathcal{C}_i} \frac{\tilde{a}_{ij}}{F_j} M_j \right] M_i$$

is Lipschitz continuous for $i = 1, \dots, s$. For Lipschitz continuity, it is sufficient to demonstrate that every partial derivative of $f_i(M_1, M_2, \dots, M_s)$ is bounded, which can be shown by computation, provided that $M_i \geq 0$ for all i . This is because when $M_i \geq 0$, $F_j \geq 1$. This non-negativity of M_i is shown in Lemma 1 below.

Thus $f_i(M_1, M_2, \dots, M_s)$ is Lipschitz for $i = 1, \dots, s$ and we have that the solution $\{M_i(t; M_1^0, \dots, M_s^0)\}_{i=1}^s$ to the initial value problem (1) is continuous in the s -dimensional domain of initial conditions $(M_1^0, M_2^0, \dots, M_s^0)$. Hence $M_1(t; \bar{M}_1^0, \dots, M_s^0)$ is continuous in the $s - 1$ -dimensional domain of initial conditions (M_2^0, \dots, M_s^0) for fixed values $\bar{M}_1^0 \geq 0$.

We finally note that $M_1(t; \overline{M}_1^0, \dots, M_s^0)$ is continuous for fixed values $t = t_1, \dots, t_d$. Hence the cost function (2) is a finite sum of continuous functions and therefore continuous. We have the desired result, that $C(M_2^0, \dots, M_s^0)$ is a continuous function, and our minimization problem must have a solution.

Lemma 1. *If $M_i(t; M_1^0, \dots, M_s^0)$ is a solution to (1) where $M_i^0 \geq 0$ for all i , then $M_i(t; M_1^0, \dots, M_s^0) \geq 0$ for all i and $t \geq 0$.*

Proof. Let $M_i(t; M_1^0, \dots, M_s^0)$ be solutions to (1) such that $M_i^0 \geq 0$ and $1 \leq i \leq s$. For brevity, we will denote this solution by $M_i(t)$ and we will introduce alternative indices ζ_z for the populations, such that $z = 0, 1, \dots, s$ and $\zeta_z = 0, 1, \dots, s$. At some time t^1 , suppose at least one population is the first to reach the boundary of this region. We denote this population with the index ζ_1 , where $M_{\zeta_1}(t^1) = 0$. For all $i \neq \zeta_1$, we still have that $M_i(t^1) \geq 0$ and so

$$r_{\zeta_1} - x_{\zeta_1} - \sum_{j \in \mathcal{C}_{\zeta_1}} \frac{\tilde{a}_{\zeta_1 j}}{F_j} M_j \geq m$$

for some $m > -\infty$. Then we have

$$f_{\zeta_1} = \left[r_{\zeta_1} - x_{\zeta_1} - \sum_{j \in \mathcal{C}_{\zeta_1}} \frac{\tilde{a}_{\zeta_1 j}}{F_j} M_j \right] M_{\zeta_1} = 0$$

because $M_{\zeta_1} = 0$, and so M_{ζ_1} will remain at the boundary. We note that if multiple populations reach the boundary simultaneously, we have the same result for every population which reaches the boundary.

Now, at some time t^{n+1} , suppose that n populations $M_{\zeta_1}, M_{\zeta_2}, \dots, M_{\zeta_n}$ have reached and remained at the boundary. Let $M_{\zeta_{n+1}}$ be the next population to reach the boundary, such that $M_{\zeta_{n+1}}(t^{n+1}) = 0$. Then for any $i \notin \{\zeta_1, \zeta_2, \dots, \zeta_n\}$, we have $M_i(t^{n+1}) > 0$, since these populations have not reached the boundary. Since $M_{\zeta_1}, M_{\zeta_2}, \dots, M_{\zeta_n}$ remained at the boundary, we have for any $i \in \{\zeta_1, \zeta_2, \dots, \zeta_n\}$ that $M_i(t^{n+1}) = 0$. Then the quantity

$$r_{\zeta_n} - x_{\zeta_n} - \sum_{j \in \mathcal{C}_{\zeta_n}} \frac{\tilde{a}_{\zeta_n j}}{F_j} M_j$$

is again bounded below, because $M_i(t^{n+1}) \geq 0$ for all $i \neq \zeta_{n+1}$. Then because $M_{\zeta_{n+1}} = 0$, we must have

$$f_{\zeta_{n+1}} = \left[r_{\zeta_{n+1}} - x_{\zeta_{n+1}} - \sum_{j \in \mathcal{C}_{\zeta_{n+1}}} \frac{\tilde{a}_{\zeta_{n+1} j}}{F_j} M_j \right] M_{\zeta_{n+1}} = 0,$$

and so $M_{\zeta_{n+1}}$ will remain at the boundary. We can therefore see that for all $i = 1, \dots, s$, if M_i reaches the boundary $M_i = 0$, it will remain at that boundary. In particular, this means that solutions to (1) with non-negative initial conditions will remain non-negative for all time.

Appendix S2: Numerical Methods

We solve the constrained optimization problem detailed in *Methods: Optimizing predator communities* using the MATLAB function `fmincon` with the `interior-point` algorithm option. Model solutions for this optimization problem are obtained using the `ode45` numerical integrator. For each optimization problem, we use the `multistart` function to solve the problem for 100 random initial iterates in the admissible space of initial predator densities. Results were generated using MATLAB R2014b, version 8.4.0.150421, on an SMP Linux operating system, version 2.6.32-75.46.3.el6.x86-64.

Appendix S3: Model Parameters

Table S1: Species-specific quantities used in simulations. Body masses and initial population densities were averaged from field data. The value of R_j was selected such that all predators are 100% successful when hunting aphids.

Species	Body mass (mg)	Initial Density (ind/ m^2)	R_j
<i>R. padi</i>	0.59	7.4111	—
<i>Pterostichus</i>	89.49	0.0152	151.68
<i>Harpalus</i>	58.11	0.0296	98.49
<i>Poecilus</i>	45.57	0.0131	77.24
Other Carabid	6.25	0.1657	10.59
<i>Bembidion</i>	1.47	0.4353	2.50
Other Spider	12.42	0.0070	21.06
<i>Lycosidae</i>	11.86	0.5565	20.11
<i>Tetragnathidae</i>	1.96	0.0063	3.32
<i>Linyphiidae</i>	1.33	0.2716	2.25

Table S2: Parameters used in simulations.

a_0	ϕ	c_0	h_0	b_0	x_0	E	T	r_1	n
0.17	1.00	[0,1]	0.12	[0,10]	$e^{24.44}$	0.686	[15,45]	0.3402	30

Table S3: ν_{ij} for all species in the simulation when predators have “high diversity” in foraging area (different foraging area for all predator species). Each column corresponds to a row (starting with *R. padi* on the left and going to *Linyphiidae* on the right).

<i>R. padi</i>	1	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
<i>Pterostichus</i>	0.6	1	0.7	0.7	0.7	0.7	0.2	0.2	0.2	0.2
<i>Harpalus</i>	0.6	0.7	1	0.7	0.7	0.7	0.2	0.2	0.2	0.2
<i>Poecilus</i>	0.6	0.7	0.7	1	0.7	0.7	0.2	0.2	0.2	0.2
Other Carabid	0.6	0.7	0.7	0.7	1	0.7	0.2	0.2	0.2	0.2
<i>Bembidion</i>	0.6	0.7	0.7	0.7	0.7	1	0.2	0.2	0.2	0.2
Other Spider	0.6	0.2	0.2	0.2	0.2	0.2	1	0.7	0.7	0.7
<i>Lycosidae</i>	0.6	0.2	0.2	0.2	0.2	0.2	0.7	1	0.7	0.7
<i>Tetragnathidae</i>	0.6	0.2	0.2	0.2	0.2	0.2	0.7	0.7	1	0.7
<i>Linyphiidae</i>	0.6	0.2	0.2	0.2	0.2	0.2	0.7	0.7	0.7	1

Table S4: ν_{ij} for all species in the simulation when predators have “medium diversity” in foraging area use (two different types of predator foraging area).

<i>R. padi</i>	1	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6	0.6
<i>Pterostichus</i>	0.6	1	1	1	1	1	0.2	0.2	0.2	0.2
<i>Harpalus</i>	0.6	1	1	1	1	1	0.2	0.2	0.2	0.2
<i>Poecilus</i>	0.6	1	1	1	1	1	0.2	0.2	0.2	0.2
Other Carabid	0.6	1	1	1	1	1	0.2	0.2	0.2	0.2
<i>Bembidion</i>	0.6	1	1	1	1	1	0.2	0.2	0.2	0.2
Other Spider	0.6	0.2	0.2	0.2	0.2	0.2	1	1	1	1
<i>Lycosidae</i>	0.6	0.2	0.2	0.2	0.2	0.2	1	1	1	1
<i>Tetragnathidae</i>	0.6	0.2	0.2	0.2	0.2	0.2	1	1	1	1
<i>Linyphiidae</i>	0.6	0.2	0.2	0.2	0.2	0.2	1	1	1	1

Table S5: Average number of species in optimal predator communities (taken over temperatures between $T = 15^\circ C$ and $T = 45^\circ C$) for varying levels of intraguild interference (b_0) and intraspecific competition (c_0).

	$c_0 = 0.01$	$c_0 = 0.1$	$c_0 = 0.3$	$c_0 = 0.5$	$c_0 = 0.7$	$c_0 = 0.9$
$b_0 = 0.1$	4.00	4.86	6.00	6.71	7.43	8.00
$b_0 = 1.0$	3.57	4.43	5.86	6.71	7.14	7.86
$b_0 = 3.0$	2.43	4.00	5.57	6.29	6.71	7.43
$b_0 = 5.0$	2.14	3.86	5.00	6.00	6.29	7.14
$b_0 = 7.0$	2.00	3.86	4.57	5.86	6.43	6.86
$b_0 = 9.0$	1.86	2.86	4.29	5.57	6.29	6.43