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Effects of Natural Enemy Biodiversity on the Suppression of Arthropod Herbivores in Terrestrial Ecosystems

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Key Words

carnivores, meta-analysis, parasitism, parasitoid, pest control, predation, predator, species richness

Abstract

Claims about the role of predator diversity in maintaining ecosystem function and providing ecosystem services such as pest control are controversial, but evaluative tests are beginning to accumulate. Empirical and experimental comparisons of species-rich versus species-poor assemblages of entomophagous arthropods and vertebrates range from strong suppression to facilitative release of herbivorous arthropod prey. Top-down control can be strengthened when natural enemies complement each other, dampened by negative interactions, balanced by both factors, and driven by single influential species. A meta-analytic synthesis shows a significant overall effect of enemy richness increasing top-down control of herbivores, which is consistent in agricultural studies conducted in tropical versus temperate zones, in studies using caged versus open-field designs, but not so in nonagricultural habitats. Synthetic analyses address theory and help set precautionary policy for conserving ecological services broadly, while characterizing uncertainty associated with herbivore response to changes in enemy diversity.

Natural enemies of herbivores:
organisms such as predators, omnivores, and pathogens that consume organisms that feed on plant foliage, roots, seeds, pollen, etc.

INTRODUCTION

Recent interest in the conservation of natural enemies of herbivores derives its theoretical roots from the 1950s and 1960s literature on community structure, diversity, and stability (Hairston et al. 1960, MacArthur 1955). Critical concerns about species invasions and species losses are often expressed in terms of preserving ecosystem function and providing ecosystem services through maintaining biodiversity (Chapin et al. 2000, Hooper et al. 2005, Lubchenco 1991, Stachowicz et al. 2007). However, our knowledge of the role of biodiversity in maintaining ecosystem function is based in plant diversity literature where emergent or aggregate functions of ecosystems are often measured as primary productivity (Balvanera et al. 2006, Hooper et al. 2005, Loreau et al. 2001). Expanding our understanding of biodiversity in ecosystem processes or the value of biodiversity to humans requires attention to higher trophic levels because plants are embedded in complex food webs of herbivores, omnivores, and carnivores. We focus this review on the role of carnivore diversity, specifically the species richness of entomophagous (insect-feeding) vertebrates and arthropods, on the suppression of arthropod herbivores in terrestrial ecosystems. Arthropod herbivore suppression by their natural enemies involves at least 50% of all species on earth (Waage 1991) and is a fundamental process for both ecosystem function and ecosystem services, spanning a rich array of cases and analyses in theoretical and applied ecology.

Although most herbivore populations are regulated by a combination of abiotic and biotic factors, including natural enemies, some are responsible for recognized outbreaks and defoliation events worldwide—with measurable impacts on ecosystems (Barbosa & Schultz 1987). Life table analyses of a wide range of arthropod herbivore species indicate that predators and parasitoids are their most frequent source of mortality, complementing the less dramatic pathogenic, abiotic, and plant-based factors, at least among immature stages (Cornell & Hawkins 1995, Hawkins et al. 1997). Top-down control implies that some measure of the suppression of an herbivore population is primarily due to mortality induced by the herbivore's natural enemies. Herbivore suppression does not necessarily indicate density dependent regulation. The degree to which predators and parasitoids suppress herbivore populations potentially affects net primary productivity, crop yield, plant composition, age structure, and diversity, as well as nutrient cycling through modulated plant consumption and processing rates (e.g., Parish et al. 1999; Schmitz 2006, 2007; Snyder et al. 2005). Given that changes in herbivore suppression may be viewed as positive or negative depending on the context, in this review we do not assign normative values to top-down regulation of herbivore populations, but instead investigate the relationship between predator species richness and prey suppression.

The species richness of predators and parasitoids fluctuates over time and space in the absence of direct human activity as well as in response to anthropogenic activities such as habitat loss, disturbance regimes, or specific management practices that degrade habitats and limit key resources for entomophagous species worldwide (e.g., Butler et al. 2007, Hendrickx et al. 2007, Landis et al. 2008, Wickramasinghe et al. 2004). Attwood et al. (2008) demonstrated that, globally, the richness of carnivorous arthropods was significantly greater in native vegetation than in agriculture as well as in reduced-input cropping systems compared to conventional agriculture. Although pesticide usage is clearly harmful to natural enemies (e.g., Purcell et al. 1995), introductions of natural enemies for biological control occasionally can cause local loss of predatory species (Carvalho et al. 2008). Natural enemy introductions, whether intentional or accidental, add a slow but not necessarily insignificant trickle of new predators and parasitoids to both managed and unmanaged ecosystems. Approximately 2000 arthropod species (mostly parasitoids) have been introduced as biological control agents worldwide (van Lenteren et al. 2006) with over 160 arthropod predators and parasitoids and 16 avian predators released in the United States by the 1980s

(Long 1981, Waage 1991). Snyder & Evans (2006) and Kenis et al. (2009) reviewed cases in which entomophagous predators and parasitoids that were added to existing enemy assemblages either suppressed, eliminated, or elevated herbivore populations through consumption, protection, or interference activities in terrestrial ecosystems. Widespread stochastic change, as well as human-associated modification of natural enemy communities, is the rule rather than the exception, and more dramatic changes are expected in the context of global climate change as extreme weather events disproportionately affect natural enemies more than herbivores (Stireman et al. 2005b) and as distributions of species shift and communities reassemble (Vance-Chalcraft et al. 2007).

To address the effects of natural enemy diversity on arthropod herbivore suppression in terrestrial habitats, we begin with an overview of the mechanistic pathways that emerge in multispecies enemy assemblages. We then present a series of empirical and experimental approaches that have been used to test the impact of natural enemy diversity on arthropod herbivores and point out the limitations inherent in different methodologies. Next, we offer a meta-analysis of published studies to synthesize what we know about the relationship between natural enemy richness and herbivore suppression. Finally, we summarize the overall findings and suggest future research directions for filling critical knowledge gaps about the effects of natural enemy diversity in complex communities across a variety of habitats.

EMERGENT EFFECTS OF NATURAL ENEMY ASSEMBLAGES

Inquiry regarding the effect of biodiversity on ecological function began at the producer level (Hooper et al. 2005, and references therein). Many studies show that increasing plant species richness leads to enhanced primary productivity or overyielding through species complementarity or a sampling effect (Huston 1997, Loreau et al. 2001, Stachowicz et al. 2007). This producer-level evidence has formed the basis for developing theory of consumer-level effects on herbivore suppression. When applied to higher trophic levels, the species complementarity model suggests that herbivore mortality resulting from the combined action of different natural enemy species is equal to (additive) or greater than (synergistic) the summed mortality caused by each natural enemy species on its own (Snyder et al. 2005, Stireman et al. 2005a). Complementary niche-related differences among natural enemies include: preying on different life stages of an herbivore, exploiting prey at different times in the season (additive effects), or foraging in ways that facilitate prey capture by other natural enemies (synergistic effect) (**Figure 1**). Negative interactions among enemies, however, such as intraguild predation, facultative hyperparasitism, or behavioral interference, may have subtractive effects on herbivore suppression (Rosenheim 2007, Schmitz 2007). If agonistic interactions among natural enemies emerge instead of complementary ones, the addition of natural enemy species may release herbivore populations from predation or parasitism pressure and possibly lead to outbreaks (Perez-Lachaud et al. 2004, Rosenheim et al. 1999).

In cases where a particular natural enemy species inflicts most of the mortality on a given herbivore (e.g., relatively greater abundance, searching ability, fecundity, longevity, or competitive ability), then it is the presence or absence of this superior natural enemy that is critical to herbivore suppression. The sampling effect model simply suggests that as species richness increases, so does the probability that a superior natural enemy species will be present in the mix (Myers et al. 1989, Perfecto et al. 2004, Stireman et al. 2005a). This sampling effect does not require any of the assumptions about complementarity to be met, yet yields a similar outcome, on average, of stronger top-down control of herbivores as enemy species richness increases (**Figure 1**). Of course, the opposite may occur (also called selection effects; Loreau & Hector 2001), whereby the probability of including a strongly disruptive natural enemy can increase as species richness increases (**Figure 1**). For example, an increase in natural enemy diversity could increase the

Species complementarity model: combined mortality imposed by multiple species is equal to (additive) or greater than (synergistic) the summed mortality from each species alone

Intraguild predation: a special case of omnivory in which a predator consumes another predator that shares the same prey species

Sampling effect model: an increase in species richness increases the probability that a particularly influential species will be present in an assemblage

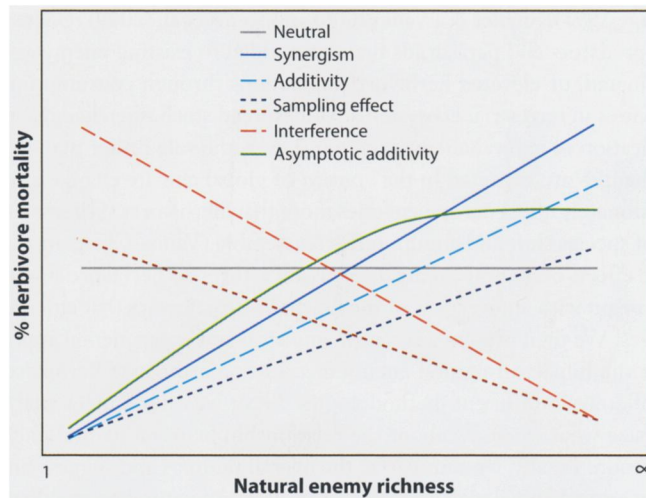


Figure 1

Possible emergent effects of natural enemy diversity on the strength of herbivore suppression or the size of herbivore populations depending on whether the interaction among natural enemy species is positive (either by additive, synergistic, or positive sampling effect), neutral (either by minimal interaction or cancelling effects of positive and negative interactions), or antagonistic (via interference through intraguild predation, competition, disturbance, or negative sampling effect) depicted as linear, but which may be nonlinear (example of asymptotic additivity effect in *green*).

chance of a debilitating competitive interaction between a superior and inferior natural enemy. If the addition of a less effective predator or parasitoid disrupts a more effective species, the probability of decreased herbivore mortality may increase with natural enemy diversity. These scenarios, in which negative interactions among natural enemies increase as diversity increases, have plagued classical biological control efforts by forcing practitioners to decide between releasing a single, presumed superior natural enemy species or multiple species against a pest (Bellows & Hassel 1999). However, in many cases, a diverse assemblage of natural enemies that includes intraguild predator species suppresses herbivore densities to a greater extent than a species-poor assemblage that lacks intraguild predators (Colfer & Rosenheim 2001, Vance-Chalcraft et al. 2007).

The insurance model emphasizes the positive interactions among natural enemies, at least of different functional guilds, predicting that additivity, synergism, and superiority will prevail, given a sufficient richness within functional groups to cover heterogeneous conditions and potentially overcome disruptive and negative interactions (Naeem & Li 1997, Yachi & Loreau 1999). Like the positive outcome of a sampling effect model, the insurance model suggests that, on average, an effective mix of natural enemies is more likely to be present under any given set of conditions as natural enemy species richness increases (Perfecto et al. 2004). However, the insurance model differs from sampling effect in that functional redundancy is a central concept. That is, in the face of conditions adverse to particular natural enemy species, key functional groups will be maintained by the presence of other species, thus ensuring herbivore suppression.

Enhanced natural enemy diversity should increase herbivore mortality when positive interactions are stronger than negative interactions among natural enemies or when superior enemies are better represented in the species pool than are disruptive ones (Figure 1). To illustrate why a change in species richness can have relatively unpredictable outcomes, Figure 2 models three terrestrial communities with different interactive effects. Compared to a moderate level of

Insurance model: the more species present, the greater chance of maintaining consistent, positive effects over the course of contingencies associated with environmental variability



Figure 2

Level of herbivore suppression owing to natural enemies shown by thickness of consumption arrows and size of circular endpoints for (a) a moderate level of herbivore suppression by complex of natural enemies associated with a single plant species, (b) an increased level of herbivore suppression caused by the addition of a specialist predator, or (c) a decreased level of suppression caused by the addition of a generalist predator that exhibits intraguild predation. Size of plant represents potential top-down diversity cascade effects.

herbivore suppression (**Figure 2a**), the addition of specialist natural enemies can increase herbivore suppression in an additive manner (**Figure 2b**). This hypothetical case allows the added natural enemy species to reduce the insectivorous bird species' food supply, possibly because the added natural enemy attacks a smaller developmental stage of the herbivore, thus reducing the abundance of larger prey and causing the bird to shift some of its foraging effort to another herbivore species. However, herbivore release may occur if the added enemy is an intraguild predator whose consumptive effect on another natural enemy in the system reduces herbivore mortality (**Figure 2c**). Therefore, an overall positive effect of natural enemy biodiversity on herbivore suppression, pest control, and ecosystem function has been claimed, questioned, and debated on theoretical and practical grounds (e.g., Bruno & Cardinale 2008, Casula et al. 2006, Letourneau & Bothwell 2008, Wilby & Thomas 2002).

NATURAL ENEMY SPECIES RICHNESS AND FUNCTIONAL DIVERSITY

To begin to answer questions about the role of natural enemy biodiversity on herbivore suppression, we must first ask, "How many natural enemy species are associated with a particular herbivore?" However, accurate numbers are almost always unavailable and often unknowable. Existing lists tend to be incomplete or unreliable because some or all taxonomic groups have not been censused, rare species are underrepresented, and accurate feeding records are sparse beyond enemies of particular herbivore species that are either economically important or represent well-studied model systems (van Veen et al. 2006). In addition, undescribed species of arthropod natural enemies are commonly encountered, even in agricultural fields.

A particularly thoroughly developed food web for birds, arthropods, and pathogens associated with broom in England shows that the majority of 23 herbivores recorded at a study site each have 13 or more natural enemy species (Mommott et al. 2000). Other estimates suggest higher species richness counts, with glassy-winged sharpshooter found in the guts of over 15 families of spiders and insects in California (Fournier et al. 2008), Colorado potato beetle consumed by 13–16 predatory arthropods and 4 parasitoids—in its native Mexico (Cappaert et al. 1991), and onion maggots associated with 86 natural enemy species in experimental plots, including 7 species of parasitoids that emerged from these flies and 21 predator species that fed on eggs, larvae, or pupae as food in laboratory arenas (Tomlin et al. 1985). In addition, both above- and belowground herbivores are likely to be fed upon by many species of vertebrate predators (Martin et al. 1951), and over 220 avian species in North America have been reported to consume insects considered pests in agricultural systems (Kirk et al. 1996).

Consequently, we may ask, “To what degree are natural enemies shared among different herbivore species?” A suite of 60 parasitoid species and 6 predatory inquiline species were associated with sawfly galls of the genus *Pontania* on willows in central Europe (Kopelke 1994). Each species of gall-making sawfly hosts 1 to 7 species of specialist parasitoid and shares many more of the 3 dominant, 18 subdominant, and 45 sporadic parasitoids and gall-dwelling predators (including beetles and moths) with other sawflies, leafminers, and other willow herbivores. Thorough accounts such as this one suggest that herbivores share many natural enemy species. Such a large number of predatory and parasitoid species has allowed for numerous enemy diversity combinations in experimental manipulations. However, herbivore suppression levels with factorial combinations of a manageable number of species (e.g., <5) may not accurately predict the effects of natural enemy species loss or gain in ecosystems.

Characterizing enemy diversity or representing it in constructed assemblages may require attention to factors beyond the number of species that share prey. Although species richness has been a common metric for researchers investigating diversity effects on ecosystem function, a more course-grained categorization of functional groups has revealed clearer patterns in many cases, at least for plants, indicating that there can be some level of functional redundancy among species for certain attributes of ecosystem processes (Balvanera et al. 2006). As a hypothetical example, entomophagous functional groups might include diurnal and nocturnal generalist predators (robber flies, flycatchers, bats) that capture prey in flight; specialist koinobiont parasitoids, whose larvae develop as their hosts feed and wander; or generalist arthropod predators using sessile traps to capture prey. Each of these functional groups could contribute to the mortality of the same herbivore species (Wilby et al. 2005). Whether the number of species within a functional group predicts the durability of this function for herbivore suppression, an assumption of the insurance model, depends on the degree to which the mechanisms driving changes in richness are functionally specific. For example, Schweiger et al. (2007) found that agricultural intensification caused extirpation of species unevenly across functional groups of syrphid fly predators: specialists were lost as a result of habitat degradation, whereas generalist species persisted. However, a priori determinations of functional groups may also be an underestimate of functional diversity if true functional diversity is fine-grained enough to be represented by species richness, even within closely related predators (e.g., MacArthur 1958, Resetartis & Chalcraft 2007).

Hooper et al. (2005) caution that despite the usefulness of a functional diversity approach, the practice of defining functional groups and quantifying functional diversity can be difficult. It may be valuable to incorporate nontrophic effects such as phenology, population dynamics, microhabitat distributions, and other relevant variables to assign species to ecologically meaningful functional groups and to use standard quantitative statistical methods to examine similarities and differences in feeding relations or substrate utilization (Bengtsson 1998, Martinez 1996). Because species

Functional diversity: the number of feeding or life-history guilds, or the relative distribution of individuals or species among those guilds

richness is the most common metric used to describe the diversity of natural enemy assemblages in the literature, we structured our meta-analysis (see below) to investigate natural enemy richness but recognize that attention to the designations of meaningful functional groups may be needed to better predict the outcome of species losses or gains on herbivore suppression levels.

EMPIRICAL AND EXPERIMENTAL APPROACHES FOR EVALUATING DIVERSITY EFFECTS ON HERBIVORE SUPPRESSION

Among the several approaches for determining if natural enemy diversity acts to enhance suppression of herbivores, reality and robustness tend to decrease as variable isolation and precision increase. Here, we provide examples of different empirical and experimental tests to illustrate how a variety of approaches might allow for stronger inferences and broader interpretations of the role of natural enemy diversity than any one alone. These different approaches include natural, seminatural, field-enclosure, and laboratory-enclosure experiments. Natural and seminatural experiments usually involve comparative measurements of mortality or survivorship of herbivore populations that differ in associated natural enemy diversity because of some environmental factor. These experiments represent an attempt to quantify realistic changes among different food webs. Direct experimental manipulation of natural enemy richness, usually carried out in enclosures, comprises the most rigorous tests for elucidating mechanisms. If the contribution of each natural enemy species to herbivore suppression can be determined alone and in combination, the roles of complementarity, cumulative negative interactions, and qualitatively different sampling effects can be determined.

Empirical measurements of herbivore suppression parameters in relatively species-rich versus species-poor natural enemy assemblages have been documented from different geographical locations that lie within the native range of an insect herbivore (e.g., Stone et al. 1995) as well as in native versus exotic locations (e.g., Cornell & Hawkins 1995). Some comparative field tests involve manipulations or disturbances that indirectly affect natural enemy richness, such as insecticide applications (e.g., Purcell et al. 1995, Ruberson et al. 1994) or other agricultural management practices (e.g., Chang & Snyder 2004, Letourneau 1987). In most comparative experiments reporting natural enemy richness, enemy abundance is either unknown or positively correlated with richness. Herbivore population abundance responds to factors other than top-down pressure in these experiments as well, sometimes in direct response to factors that cause changes in natural enemy richness. Because of possible hidden treatments (*sensu* Huston 1997), often the only conclusion that can be made from a natural experiment showing a positive relationship between enemy richness and herbivore suppression is that any negative interactions among predators could not have outweighed complementarity, positive sampling effects, or confounding enemy abundance effects that may have been present in the richer assemblage (see Cardinale et al. 2006b).

Semimanipulative field tests control for changes in herbivore abundance by using sentinel herbivores. That is, a determined number of herbivores is placed into field conditions as a means of detecting relative predation or parasitism activity by natural enemy assemblages differing in species richness (e.g., Armbrrecht & Gallego 2007). Tylianakis et al. (2008), using a standard number of nest sites, found that parasitism rates on eumenid wasps (pollen and nectar feeders) were positively associated with parasitoid richness independent of habitat type in replicated rice, pasture, coffee, abandoned coffee, and forest plots. Alternatively, the measurement of a wide range of parameters in unmanipulated field studies can allow for the detection of certain hidden treatment effects through path analysis measurements of relative interaction strengths (see Dyer & Stireman 2003).

Manipulative experiments have used substitutive and/or additive changes in natural enemy richness, often with factorial designs, to compare herbivore suppression by single enemies and

Suppression of herbivores: increased mortality resulting in decreased population size compared to some standard, such as outbreak or economic threshold level

in combinations. As a result, it is now clear that a full spectrum of interactions is possible within a complex of natural enemies (Casula et al. 2006): additive and synergistic interactions due to resource partitioning or complementary foraging modes (Borer et al. 2004, Losey & Denno 1998, Snyder et al. 2008, Wilby et al. 2005) and antagonistic interactions due to intraguild predation or interference (Rosenheim et al. 1993). Straub & Snyder (2006) found that the inclusion of a highly effective species in multiple predator complexes was the key driving force behind the positive relationship between natural enemy diversity and aphid control, which was consistent with the sampling effect. Wilby et al. (2005) found greater predation rates by a three-species assemblage of predators than by any single predatory species alone where each predator consumed different larval stages of the prey, leading to functional complementarity. However, Halaj et al. (1997) demonstrated that permitting ant foraging reduced salticid spider abundance, likely through some combination of intraguild predation and interference competition. Snyder & Wise (1999) found that when lycosid spiders were present with carabid beetles, no intraguild predation took place, but spiders altered their feeding habitats and eventually emigrated.

Synergistic or additive effects among natural enemies (**Figure 1**) imply that herbivores suffer mortality that is distributed among two or more enemy species. A relatively even distribution pattern for top-down control is commonly observed. For example, in France, parasitism of field-collected alfalfa blotch leafminer fly larvae was divided among a diverse suite of species, yielding parasitism rates in the range of 70–90% (Dureseau & Jeandel 1977). In contrast, similar mortality rates of a confamilial leafminer hosting 25 parasitoid species were determined primarily by a single polyphagous parasitoid attacking the pupal stage (Kato 1994). Such asymmetrical mortality patterns among natural enemies or clear dominance of a single species are also widely reported (e.g., Costamagna et al. 2008, Hooks et al. 2003, McClure 1986, Mols & Visser 2002). Food web data on herbivores that occur on the same plants showed a relatively even level of parasitism of green peach aphids among four or five primary parasitoid species, whereas cabbage aphids were parasitized primarily by a single species (Bukovinszky et al. 2008). Asymmetric levels of mortality among natural enemies may imply important identity factors such that a sampling effect mechanism would be more likely than cumulative effects. Therefore, herbivores in the presence of a strongly superior natural enemy species might be more strongly suppressed via the sampling effect than by enemy species richness *per se*.

It is unclear how much the results of highly manipulative cage studies can tell us about what to expect in forest or grassland ecosystems, or even in agricultural production systems that also encompass a wide range of natural enemy taxa and functional groups. Whereas manipulations comparing herbivore consumption rates of a single natural enemy with those of two or three enemies together allow for detailed quantitative comparisons that can distinguish additive from sampling effects, very few populations of phytophagous insects will be subject to only one natural enemy species. In addition, the composition of experimental assemblages is often neither random nor based on observed (or predicted) composition changes in real systems. Therefore, we include these targeted experimental studies in a meta-analysis along with a broader array of manipulations and empirical field studies comparing herbivore suppression levels or herbivore abundance under varied levels of natural enemy richness.

META-ANALYSIS—IMPACTS OF NATURAL ENEMY DIVERSITY ON HERBIVORE ABUNDANCE AND MORTALITY

We used a quantitative synthesis to arrive at a generalized conclusion about whether a measurable effect of natural enemy richness on herbivore suppression exists, and if it does, to determine whether the direction of these effects is positive or negative. A finding of greater suppression

of herbivores with higher natural enemy species richness would imply that complementary or positive selection effects in relatively species-rich natural enemy assemblages are more prominent or stronger than interference or negative selection. Findings of lesser suppression of herbivores would imply the opposite is true. A meta-analysis of a sample of independent studies from the literature can be used to resolve broad ecological questions such as this one when individual hypothesis tests are considered conceptual replicates and is an appropriate method to analyze and compare findings of different strengths across studies (Lipsey & Wilson 2001). An alternative interpretation is that the effect size derived from each individual test represents a true effect size, and the raw distribution of these effect sizes best represents the answer to the larger question. Therefore, we report the distribution of effect sizes (magnitude and directions) for individual tests of natural enemy diversity and herbivore suppression, an overall effect size for the collection of tests, and effect sizes for major ecosystem types and experimental designs. The latter effect sizes compare agricultural and nonagricultural communities, tropical and temperate systems, and field versus cage experiments. In addition, we examined herbivore population parameters measured and experiment duration as potential biases among the studies.

The meta-analysis is based on data from 62 published papers that included some measure of herbivore mortality or relative abundance (e.g., number of individuals remaining, or percent parasitism under two or more conditions of natural enemy species richness). Some of these studies directly manipulated predator species richness under controlled conditions, some manipulated other factors (e.g., vegetation) that indirectly affected natural enemy richness, and others were comparisons among locations or habitats that differed in natural enemy richness. All studies were conducted in terrestrial systems and satisfied the following criteria: (a) species richness of vertebrate and/or arthropod natural enemies was greater than zero in all comparisons, thus excluding studies that compared presence versus absence of natural enemies; (b) predator and/or parasitoid species richness was quantified or manipulated in a way that could be construed as relatively species-rich versus species-poor conditions for the prey or host herbivore(s); (c) arthropod herbivore abundance or mortality parameters associated with changes in natural enemy species richness were measured; and (d) researchers reported means for arthropod herbivore response variables, variance around the means, and numbers of replicates. In some cases, missing information was obtained by contacting researchers. Several papers provided separate experiments involving different herbivores and/or different natural enemy manipulations, thus yielding a total of 266 comparisons. **Supplemental Appendix 1** (follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>) explains search methods, specifies criteria used to select studies for the data set, and provides references for all articles used in the analysis.

We used a column reversal marker in the meta-analysis spreadsheet (Gurevich & Hedges 1993) to include studies that measured herbivores remaining (+) and consumed (–) following exposure to natural enemies. To calculate the effect (herbivore suppression) as a proportional change of natural enemy diversity, we used bias-corrected Hedge's d to calculate the overall treatment effect size (d_+). Hedge's d is known to handle small sample sizes (n values) and is the appropriate choice when experimental and control group means differ in signs and therefore effect sizes quantified as response ratios are inappropriate (Rosenberg et al. 2000). In this analysis, a negative Hedge's d value indicates increased herbivore suppression from increased natural enemy richness. A positive value indicates the opposite effect and zero corresponds to no effect. Results were interpreted as being statistically significant if the 95% confidence intervals (CI) excluded zero. Mean effect sizes (d_+) were not weighted by their variances and were instead treated equally to remove biases against small sample sizes (e.g., Halaj & Wise 2001, Hedges & Olkin 1985). Differences in effect sizes were calculated using mixed-effects models (Gurevich & Hedges 1993) performed with MetaWin 2.0 statistical software (Rosenberg et al. 2000). Mixed-effects models were the appropriate choice

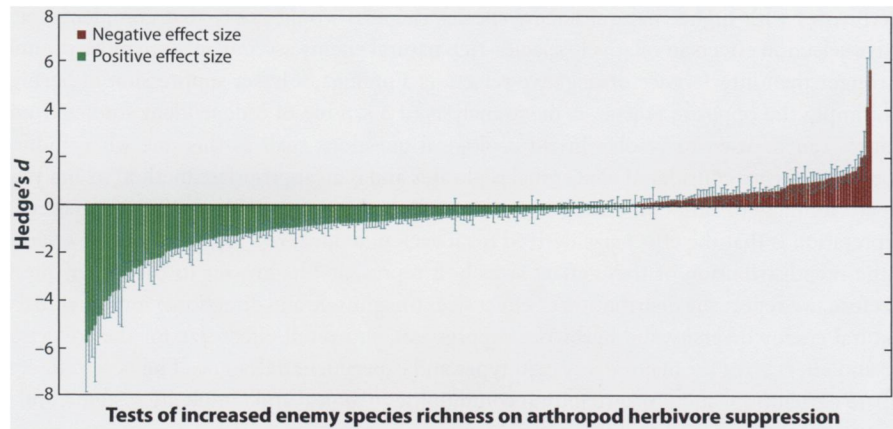


Figure 3

Hedge's d values and variances for d based on experimental and control sample sizes (see Hedges & Olkin 1985) for 266 independent tests of the effect of increased natural enemy species richness on herbivore suppression.

given the high likelihood that effect size variation would be influenced by both systematic and random components across studies. Random effects in the model can account for real effect sizes and methodological differences as well as sampling error among individual tests—potentially resulting in wider (more conservative) confidence intervals around overall effect size estimates. It is reasonable to argue that there are always at least some real (that is, substantive, not methodological) moderator variables (interactions) that create differences in real effect sizes across studies conducted in widely differing systems (Schmidt et al. 2009, Stram 1996). Meta-analyses employing random- or mixed-effects models account for random variation in true effect sizes among studies, whereas fixed-effects models assume that differences among studies are solely due to sampling error (Gurevich & Hedges 1993, Lipsey & Wilson 2001). Because standardized effect sizes were normally distributed, no resampling methods were performed (**Supplemental Appendix 2**).

For the 266 comparisons of enemy richness effects, the number or mean of natural enemy species in rich assemblages ranged from 1.2 to 35 (mean = 3.7 ± 0.2 SE) and from 0.5 to 22 (mean = 1.8 ± 0.1 SE) in comparatively species-poor assemblages. On average, the latter contained half as many natural enemy species as the former. The effect of natural enemy richness ranged along a wide gradient of both strength and direction, from strong suppressive effects on herbivorous prey to reduced mortality and release of herbivores (**Figure 3**). Of 266 comparisons of herbivore suppression, 185 yielded negative Hedge's d values (indicating a greater level of suppression with increased enemy richness), 80 were positive (herbivore suppression was dampened by enemy richness), and one had an effect size of zero (**Figure 3**). Thus, the distribution of effect sizes for enemy richness in our study was 69.5% negative (average Hedge's $d = -1.1 \pm 0.1$ SE) and 30% positive (average Hedge's $d = 0.7 \pm 0.1$ SE). In comparison, a meta-analysis on predator removal effects reported by Halaj & Wise (2001) resulted in an increase in herbivores in 77% of the cases (positive effect size) and a decline in herbivore abundance in only 20% of the experiments. They found that the average magnitude of the positive effects (herbivore release) was much larger than that for the negative cases (Hedge's $d = 1.1 \pm 0.2$ SE versus -0.3 ± 0.2 SE).

The overall effect size for our sample of studies yielded a qualitatively similar result—that an increased level of natural enemy diversity increased herbivore suppression on average ($d_+ = -0.523$, 95% CI -0.686 to -0.360 ; **Figure 4**). This outcome is robust given that, using

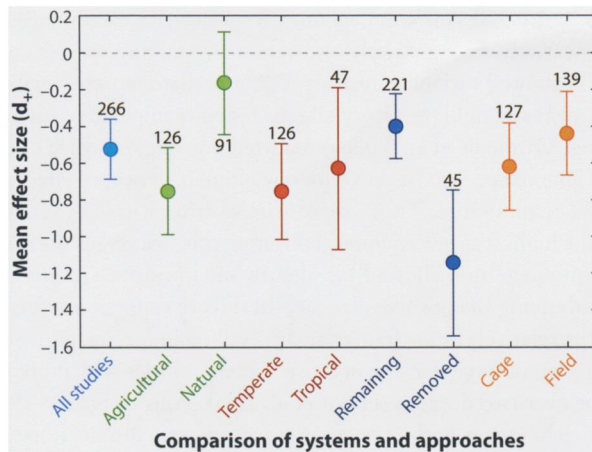


Figure 4

Mean effect size (d_+) values and 95% confidence intervals for all 266 studies and pairwise comparisons of subsets of studies used in the meta-analysis. Numeric values indicate the number of studies represented by each point. The tropical-temperate comparison includes only agricultural systems studies. The natural-agricultural comparison includes only temperate region studies.

Rosenthal's (1979) method of calculating fail-safe numbers, over 3656 comparisons with no effect (effect size = 0) would need to be added to the meta-analysis to produce a nonsignificant mean effect size (when $\alpha = 0.05$). Additionally, the normal quantile plot (**Supplemental Appendix 2**), shows no large gaps or strong nonlinear curves, indicating that our distribution of Hedge's d values (**Figure 3**) likely represents ecological phenomena rather than simple publication bias (Wang & Bushman 1998).

Halaj & Wise's (2001) meta-analysis of experiments testing for trophic cascades concluded that herbivore abundances increased as predation pressure was decreased ($d_+ = 0.77$, 95% CI 0.61 to 0.93, where their positive d values equate to our negative d values). Similar direction and strength of natural enemy diversity on herbivore suppression in our analysis of overall effect size suggest that differences in natural enemy richness played a similar role as carnivore presence or absence did in their collection of studies. Additionally, Schmitz et al. (2000) found a strong effect of carnivore removals on herbivore release but measured effect sizes using log response ratios, so a direct comparison to the strength of their result is not possible. Also, using log response ratios in a meta-analysis of enclosure studies removing predators, Van Bael et al. (2008) found a significant linear relationship between increasing species richness of insectivorous, migrant avian predators (from 3 to 11 species) and percent reduction of arthropods, although prey items were not divided into guilds such as herbivores and predators.

Some, but not all, of the meta-analyses that report an overall effect size of natural enemy species richness on herbivore suppression, rather than effect sizes derived from enemy presence/absence comparisons, have found similar unidirectional or positive effects. As in our study, an overall strengthening of herbivore suppression with natural enemy species richness was found by Stiling & Cornelissen (2005), with multiple-species introductions of biological control agents increasing insect pest mortality by 13% on average and decreasing pest abundance by an average of 27% compared to an introduction of only one new predator or parasitoid. Borer et al. (2005) found no overall effect of species richness on herbivore suppression, with the caveat that average enemy richness in comparisons may have been too low to distinguish effects (average of 3.4 and 1.4 predator species in agriculture and grasslands, respectively). By comparison, our studies averaged

3.0 (± 0.2 SE) and 4.9 (± 0.5 SE) different enemies in species-rich assemblages in agricultural and natural systems, respectively. Using strictly one versus two enemy species comparisons, Vance-Chalcraft et al. (2007) showed variable effects of adding predator species owing to a combination of complementarity and intraguild predatory effects. Using manipulative studies of three or more natural enemy species, Cardinale et al. (2006a) reported a strong, negative effect of consumer diversity on herbivore abundance—consistent with our estimate of overall effect size—for a range of aquatic and terrestrial communities. The more restrictive criteria used by Cardinale et al. (2006a), response values for the highest species richness consumer mixture versus the mean response values for those species in monoculture, allowed for identifying a positive sampling effect as the most likely mechanism underlying the positive diversity–herbivore suppression relationship.

Whether or not the relatively linear food chains prevailing in species-poor ecosystems are more likely to have stronger predatory effects than those in communities with more complex food webs has been debated for over two decades (Hulot et al. 2000, Polis & Strong 1996). We compared the effect of enemy richness on herbivore suppression in agricultural to natural systems in the temperate zone, as well as agricultural studies conducted in temperate versus tropical systems. Whereas in the temperate zone, studies increasing natural enemy richness in agricultural systems had an overall negative effect on herbivore abundance, the average effect size in natural systems did not statistically differ from zero (**Figure 4**). The similar mean effect size of agricultural studies in the temperate zone and all tropical studies (95% of which were agricultural) suggests that a suppressive effect of natural enemy diversity was widespread in agricultural systems (**Figure 4**). Stronger effects in agricultural systems as compared to natural systems are unlikely to be caused solely by differences in enemy richness among studies. Enemy richness in species-poor assemblages tended to be greater in natural and tropical ecosystems in our comparisons (Wilcoxon two-sample, one-way test, $P < 0.04$), but average enemy richness in species-rich assemblages was affected neither by habitat nor locality. Also, rich and poor assemblages differed by two natural enemy species, on average, in both temperate and tropical locations (1.6 ± 0.1 SE in agricultural, and 2.3 ± 0.2 SE in natural habitats). Focusing on abundance rather than richness effects, Halaj & Wise (2001) found that predator abundance strongly affected herbivore densities in both agricultural and natural systems, yet trickle-down effects that reduced plant biomass were only evident in agricultural systems. Whether natural enemy richness and abundance effects trade off in controlling herbivore populations in agricultural versus natural systems settings can be detected in future research through a diversity cascades approach.

Alternatively, Halaj & Wise (2001) noted that predator-enhancement manipulations, which were more common in agricultural studies, were more likely to result in large effect sizes, even though significant results persisted when predator enhancement studies were removed from their analysis. Unequal sample sizes prevent a conclusion from our data; however, studies that measured suppression by quantifying the number or proportion of herbivores remaining at the end of the experiment had smaller mean effect sizes than did studies measuring the number or proportion of herbivores removed via predation or parasitism, although both manipulations maintained the same directionality (**Figure 4**). If this difference were to be maintained with more equal sample sizes, it may be explained by natality or other parameters that affect population size and obscure direct mortality caused by natural enemies.

Although factors such as spatial heterogeneity, study venue, design, and study duration can reasonably be expected to alter the outcome of enemy diversity–herbivore suppression tests, we found no significant differences in the direction (both showing a significant effect of increased natural enemy diversity) or magnitude of the response of cage studies (conducted in field, laboratory, and greenhouse enclosures, $d_+ = -0.616$, $n = 127$, 95% CI -0.853 to -0.379) compared to field tests ($d_+ = -0.438$, $n = 139$, 95% CI -0.664 to -0.212). Nor was there a significant difference

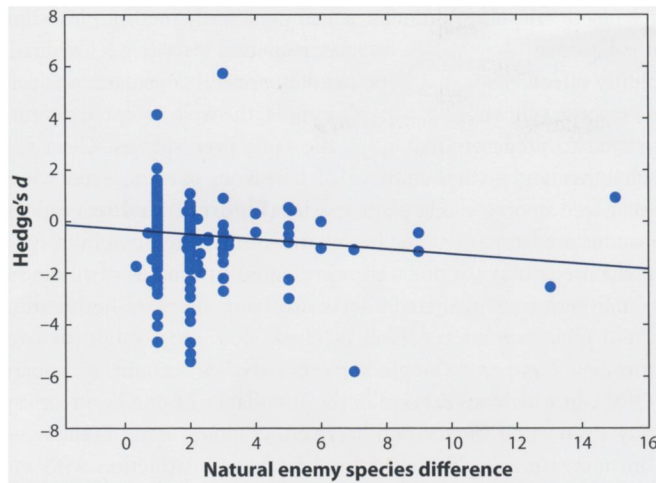


Figure 5

Difference between the species richnesses of the rich enemy mixture and the poor enemy mixture versus effect size (Hedge's d) shows a significant negative relationship, indicating an incremental increase in herbivore suppression strength with a greater magnitude of change in richness.

among substitutive designs ($d_+ = -0.350$, $n = 38$, 95% CI -0.794 to 0.094) versus additive designs ($d_+ = -0.681$, $n = 79$, 95% CI -0.984 to -0.378) or unspecified but probably additive designs ($d_+ = -0.483$, $n = 149$, 95% CI -0.702 to -0.265), however, more studies exhibiting substitutive designs may be needed to truly distinguish the role of richness versus abundance. Likewise, no significant differences were found between studies carried out for short (<10 days, $d_+ = -0.676$, $n = 91$, 95% CI -0.957 to -0.395), medium (10 to 30 days, $d_+ = -0.542$, $n = 70$, 95% CI -0.864 to -0.221), and long (31 days to 3 years, $d_+ = -0.406$, $n = 103$, 95% CI -0.669 to -0.142) periods. Study durations ranged from one day to almost three years, with an average duration of two to three months.

To test a corollary hypothesis, that the level of herbivore suppression increases with incremental differences in species richness, we ran a linear regression comparing the difference between high and low richness to effect size values. Although the magnitude of change in natural enemy species richness between relatively species-rich and species-poor enemy assemblages was an effective predictor of herbivore suppression pressure in the studies we analyzed (General Linear Models regression, $R^2 = 0.015$, $F = 4.11$, $P = 0.044$; **Figure 5**), most of the comparisons are clustered, testing the effect of smaller increments in natural enemy species richness. Consequently, the removal of a single comparison testing relatively larger differences in natural enemy species richness (Kruess & Tschardtke 1994; difference = 7, Hedge's $d = -5.817$), results in a slope statistically indistinguishable from zero. To assess more confidently the importance of incremental additions or removals of natural enemy species, more comparisons of large changes in enemy richness are needed.

ECOSYSTEM-LEVEL CONSIDERATIONS OF NATURAL ENEMY DIVERSITY ON THE MORTALITY OF HERBIVORES

Investigators have primarily considered the impact of natural enemy richness on the regulation of a single herbivore species, hoping to understand community- or ecosystem-level processes by zeroing in on one herbivore at a time. However, when ecosystem function measurements such as

Trait-mediated effects: interference or facilitation of the action of one organism by another organism, such as disruption of consumption activities through intimidation

resource use efficiency or consumption rates, which necessarily incorporate whole trophic levels, are predicted based primarily on single-species response tests (e.g., Cardinale et al. 2006a), emergent community effects may be overlooked. Theoretical considerations can be constrained by single-species response spheres, as well. For example, the well-accepted definition of intraguild predation is restricted to predators that share the same prey species. Clearly, natural enemies interact with each other and with a number of herbivore species, even when one considers only herbivores that feed upon a single plant species (**Figure 2**). Indirect effects of omnivorous enemies that consume predators of other herbivores in the same community (thus not strictly defined as intraguild predators) are not well represented by studies of single herbivore species in isolation. Yet, emergent trait-mediated effects involving alternate herbivores (Schmitz 2007) can buffer intraguild predation effects (Holt & Huxel 2007) that might be overrepresented in single herbivore studies. Neither do single herbivore studies account for apparent competition (van Veen et al. 2006), in which an increase in the abundance of one herbivore species indirectly impacts another by supporting higher numbers of a common natural enemy—the extreme of which could be an increasing likelihood of local herbivore extinction with increasing natural enemy diversity (Muller & Godfray 1999).

Moving beyond a single herbivore population to multispecies associations with herbivores and plants introduces additional dimensions of heterogeneity that both represent real ecosystems and set the stage for complex interspecific interactions. Tylianakis et al. (2008) predict that such heterogeneity may increase the strength of diversity effects on ecosystem processes such as parasitism rates of herbivores and plant pollination; and it may further contribute to the wide ranging distribution of the study results and quantitatively different outcomes for agricultural and natural system tests that we have reviewed here. Heterogenous patterns of herbivore abundance, whether direct effects of prey/host sharing among natural enemies (**Figure 2**) or indirect effects as described above, are likely to interact with enemy diversity effects. Griffiths et al. (2008) found strong positive effects of natural enemy diversity on herbivore suppression, owing to the emergence of a sampling effect when enemy abundances were low, but complementary effects gained importance when enemy abundances were moderate and high. Interference rates among natural enemy species also may change depending on host density, for example, through intensified within-host competition and host-feeding attacks (Kato 1994) or via increased bird predation of parasitized hosts (Tschardt 1992).

We recognize that a variety of factors, from logistical constraints for experimental manipulations to practical motives for target pest control, have resulted in a legacy of one predator–one prey studies that provide detailed assessments of when and how natural enemies cause mortality in prey populations while offering no community-level context (Letourneau & Andow 1999). However, food web studies provide the community context, charting numerous trophic interactions, but commonly lack details on most of the population effects and their underlying mechanisms. Taken together, the studies reviewed here represent a major effort to bridge this gap and provide both a measure of the range of outcomes that can occur as natural enemies are lost or gained from an ecosystem. How can the information generated in these studies be used for improving basic and applied knowledge about ecosystems?

Ultimately, we are faced with a fundamental question for which we now have an accumulation of cases and several synthetic generalizations. If we wish to better understand the role of biodiversity in ecosystem function, then the generalized outcome (natural enemy richness promotes herbivore suppression), one of the categorical outcomes (this generalization does not hold for studies conducted in natural or nonagricultural systems), and the variability in strength and direction among individual cases are instructive (**Figures 3 and 4**). They complement and add to the accumulated body of knowledge about trophic interactions, both informing the bigger picture and providing

grist for comparative analyses within and among ecosystem components. Policy formation regarding conservation, land use, and management practices is most aptly guided by evidence of an overall, or average, tendency of scientific findings over the wide variety of systems and conditions. If the goal is to inform conservation and land use policy, then an average tendency for herbivore suppression to increase with the number of natural enemy species in the system can be used to define and enact precautionary measures with the purpose of protecting particular ecosystem services. Quantitative syntheses of a large range of studies provide an overall magnitude of the effect, but also the precision of that estimate of magnitude, as represented by the confidence interval.

In contrast to large-scale or abstract considerations, individual design elements for a local grower to promote biological control of pests or for a park resource ecologist to enhance biological control of weeds requires attention to individual cases that may help to predict a particular outcome. The level of uncertainty for regulating a specific herbivore under any particular constellation of conditions is too high for recommendations based on general probabilities or an overall effect size derived from widely varying studies (Bruno & Cardinale 2008, Letourneau & Bothwell 2008). The past decade of research has greatly increased our knowledge about biodiversity and ecosystem function or services. However, any current paradigms or decisions are necessarily based on incomplete information and require further experimentation on larger scales and incorporating spatial, temporal, and compositional heterogeneity (Bruno & Cardinale 2008, Griffiths et al. 2008, Tylianakis et al. 2008). In the face of continuing high rates of species loss across taxa, this synthesis, and further research aimed at deepening an understanding of biodiversity's roles, can help direct the development of appropriate policies for ecosystem function and service preservation and advance theoretical treatments of complexity within ecological systems.

SUMMARY POINTS

The accumulation of research investigating the relationship between terrestrial natural enemies and herbivore suppression suggests several generalizations:

1. Species losses and introductions in natural enemy communities have unpredictable effects on herbivore suppression because of the wide range of enemy-enemy interactions (positive, negative, and neutral) that have been demonstrated to occur in terrestrial systems.
2. Different experimental approaches are necessary for elucidating biodiversity effects in ecosystems because of inherent strengths and weaknesses regarding precision, realism, and the possibility of hidden treatments among empirical and experimental comparisons. Integrative tests of biodiversity changes on multiple trophic levels will incorporate the complexity missing from single herbivore trials, such as those used currently to make generalizations about ecosystem processes.
3. Our quantitative synthesis of published studies shows that increases in natural enemy species richness, whether resulting from natural differences or experimental manipulations, yield a general result of greater herbivore suppression. This overall relationship suggests a stronger impact of positive, complementary interactions among natural enemy species over negative, antagonistic interactions in the studies we reviewed.
4. Categorical comparisons showed that agricultural system studies displayed a very strong relationship between higher enemy diversity and herbivore suppression. This strength was consistent between the temperate and tropical studies. In contrast, this relationship between enemy diversity and prey abundance or mortality was not statistically significant in nonagricultural systems.

5. Case by case considerations of the outcomes of enemy biodiversity, however, show a high level of unpredictability in the direction of the effect, with 30% of the cases illustrating herbivore release in the presence of higher enemy diversity. Therefore, caution should be used in relating the general case to any particular one in the field.
6. The majority of published studies investigate small-order changes in natural enemy richness. To strengthen the predictive impact of future study, researchers should test impacts on herbivore populations with larger differences between the species-rich and species-poor conditions.

DISCLOSURE STATEMENT

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