

Pest suppression by ant biodiversity is modified by pest biodiversity

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Summary

1. Agroecosystems are often complex ecosystems with diverse food webs. Changes in food web complexity may have important context-dependent consequences for pest control strategies.
2. The success of predator introductions to suppress pests may depend on the diversity of pests. For crops with diverse pest assemblages, it is hypothesized that diverse predator communities are needed to suppress diverse pest assemblages below damaging levels.
3. In this study, we compare the ability of ant predator monocultures and polycultures to suppress single- and diverse- (three species) pest assemblages in a coffee foodweb. We use a factorial experiment that compared treatments of predator and pest diversity to understand the impact of pest diversity on multiple predator effects.
4. We show that predator polycultures enhanced pest risk relative to predator monocultures significantly more in the diverse-pest treatment relative to in the single-pest treatments for two of three pest species. Further, we show that pest diversity significantly reduced pest risk in all predator treatments except for the predator polyculture treatment.
5. These results suggest that pest diversity may reduce the efficiency of single predator species at suppressing pest damage, but do not limit multiple predator species. This in turn leads to stronger effects of predator diversity with greater pest diversity. These results highlight the need to consider foodweb complexity,

such as pest diversity, when designing and implementing biology control programs.

Keywords

Multiple predators, pest control, ecosystem function, ecosystem service, agroecology, ant, coffee, biodiversity

Introduction

Agroecosystems are productive ecosystems that are often made up by complex and diverse food webs (Root 1973; Field *et al.* 1998; Siemann 1998; Rand, Tylianakis & Tscharntke 2006; Vandermeer, Perfecto & Philpott 2010). Making up approximately 40% of the terrestrial Earth (Foley *et al.* 2005), these ecosystems are also often temporally dynamic because of frequent disturbances caused by harvest and crop rotation (Rand, Tylianakis & Tscharntke 2006). Further, differences in the cultural practices of agricultural producers introduce substantial variation in the ecological complexity observed within agricultural landscapes (Altieri 1987; Philpott *et al.* 2008; Kremen, Iles & Bacon 2012). Understanding how this resulting variation in food web complexity influences ecosystem functions delivered by species is therefore vital to our general understanding of ecology.

Natural biological control agents suppress agricultural pests, but their success is influenced by variation in food web complexity (Finke & Snyder 2008; Tylianakis & Romo 2010; Philpott, Pardee & Gonthier 2012). Experiments that manipulate the number of predator species and observe their negative effects on the behavior and abundance of

pests (prey suppression) have often found variable results (Sih, Englund & Wooster 1998). Much research has described how that variability is often due to interactions between predators that both reduce (intraguild predation and interference competition) or enhance (niche partitioning and facilitation) the efficiency of prey suppression (Sih, Englund & Wooster 1998; Letourneau *et al.* 2009; Tylianakis & Romo 2010; Griffin, Byrnes & Cardinale 2013). While these predator-predator interactions are clearly important, there are several other factors that may contribute to the efficiency of multiple predator assemblages.

In particular, it is hypothesized that pest diversity may alter the efficiency of predator diversity (Wilby & Thomas 2002; Tirok & Gaedke 2010; Tylianakis & Romo 2010). For one, increasing pest diversity may lead to a greater dietary-resource niche space for predator species to exhibit niche partitioning. Different pest species may have different anti-predator defenses that require specialization amongst predators. Therefore, while single predator species may be dominant in capturing individual pest species, pest assemblages with greater anti-predator functional diversity will likely require more predator species. Alternative prey species may also distract predator species reducing predator efficiency in some cases (Musser & Shelton 2003; Koss & Snyder 2005). On the other hand, increased pest diversity could increase competition and intraguild predation between predators.

Given the potential for pest diversity to influence the success of diverse versus simple predator assemblages it is important to highlight that diverse pest communities exist in many agroecosystems. Indeed, many crop species have multiple economically important pest species. For instance, corn or soy monocultures in North America may

contain diverse pest assemblages of more than 20 species (O'Day and Steffey 1998, Herbert and Malone 2012). The classic study by Root (1973) describes an herbivore assemblage found on collard greens that contains up to 94 potential pest species, with five major pest species from three distinct functional groups (pit, strip, and sap feeders). This study underscores the importance of capturing the community-wide effects of predator biodiversity on pest assemblages and further demonstrates the importance of additional studies that incorporate greater pest diversity.

In this study, we use a factorial experiment to explore the efficiency of ant predator polycultures (three species) and monocultures (single species) in suppressing damage to coffee (*Coffea arabica*) by single-species and diverse- (three-species) pest assemblages. We hypothesized that ant polycultures are better at suppressing pests relative to ant monocultures in diverse pest assemblage, but not in single species assemblages. We also hypothesized that pest diversity limits the success of all predator groups, but that it would limit predator monocultures more than polycultures.

Methods

We conducted research in coffee plantations at the Finca Irlanda Research Station in Chiapas, Mexico in March-July of 2013. There, coffee agroecosystems host a great diversity of coffee arthropod herbivores and predators. We studied ant predator suppression of three pest species that ranged in size (minute, large, medium) and functional group (berry borer, leaf chewer, and sap sucker): 1) The small (<1 mm) coffee berry borer (*Hypothenemus hampei* Ferrari, 1867 [Coleoptera: Curculionidae]) is the most important arthropod pest of coffee worldwide because adults bore into coffee

berries, lay eggs, and the larvae damage the harvestable seeds (Damon 2000). 2) The large (approx. 8 mm) adults of *Rhabdopterus jansonii* (Jacoby) (Coleoptera: Chrysomelidae) chew coffee leaves and the fleshy outer parchment of berries, but rarely cause large economic damage (Barrera, Herrera & Gómez 2008; Kuesel *et al.* 2014). 3) The medium sized (approx. 6mm) *Macunolla ventralis* (Signoret 1854a: 21; [Hemiptera: Cicadellidae]) is a common polyphagous leafhopper that feeds from the xylem of coffee. While leafhopper damage to coffee is minor, some Cicadellidae are vectors of important coffee pathogens (Redak *et al.* 2004).

Coffee-ecosystems in Chiapas also host a diversity of predators (Vandermeer, Perfecto & Philpott 2010). We focused on three ant species known to suppress pests via consumptive and non-consumptive effects (Jiménez-Soto *et al.* 2013) because while ants may actively remove pests, they do not always consume them. *Azteca sericeasur* Longino (previously referred to as *A. instabilis*) is a dominant, arboreal species that dictates the structure of the food web on coffee (Vandermeer, Perfecto & Philpott 2010). *Pseudomyrmex ejectus* F. Smith 1858 and *Pseudomyrmex simplex* F. Smith 1877 are arboreal ants that nest in hollowed coffee branches. These three species suppress *H. hampei* damage (Gonthier *et al.* 2013), but their effects on other pests are relatively unknown.

To determine the effects ant richness on pest suppression, we conducted laboratory experiments using insect arenas (60×60×60cm; Bug Dorm-2, Bug Dorm Store, Taiwan). We introduced coffee branches, pests (1 or 3 species), and ant predators (0, 1, or 3 species) into arenas in a 4×5 factorial experiment (Table 1). We introduced coffee branches with undamaged leaves and berries. Due to the large size discrepancy between

pest species we were not able to perform a substitutive experiment for pest species. Pest treatments followed an additive design with single species treatments as follows: (1) for *H. hampei*, we released 20 adult individuals, (2) for *M. ventralis* we released 3 individuals, and (3) for *R. jansoni* we released 3 individuals. We released the same numbers of each pest species together in the diverse pest treatment. The densities of pests were decided based on previous research and observed densities on coffee plants in the field (Philpott, Pardee & Gonthier 2012).

Ant species treatments compared no ants, ant monocultures (*A. sericeasur*, *P. ejectus*, or *P. simplex*), and ant polycultures with a substitutive design. We held ant worker density at approximately 36 workers across the monocultures and polycultures (12 workers per species), however we also incorporated *P. ejectus* and *P. simplex* brood and twig nest material to improve normal worker activity (Philpott, Pardee & Gonthier 2012). Previous experimentation with *A. sericeasur*, *P. simplex*, and *Proccryptocerus hyleaus* found variation in two-species composition did not have differential effects on the berry borer (Philpott, Pardee & Gonthier 2012). For this reason we did not include variation in predator species composition in the predator polyculture.

To quantify pest damage after the 24h experimental duration, we counted the number of coffee berries infested by *H. hampei* and counted the number of mm² of leaf tissue damage by *R. jansoni*. Given that the stylet-feeding damage of *M. ventralis* is difficult to observe, we measured a proxy for damage as the average abundance of *M. ventralis* on coffee plant tissue at time 0.5h, 6h, and 17h from the experimental initiation. Laboratory observations suggested that 77% (20/26) of *M. ventralis* individuals placed on coffee leaves fed within 20 minutes. For the diverse herbivore treatment, we measured

the three damage types and created a ‘damage index’ by standardizing each type of damage measurement with a minimum-maximum scaling ($x' = x - \min / \max - \min$) before summing across the three damage types.

To test the hypothesis that pest diversity modifies multi-predator effects, we took a null model approach using multiplicative risk models for substitutive designs (Griffen 2006). The null model compared the observed pest damage in the predator polyculture to the expected (Exp_{poly}) given the predator monocultures:

$$(1) Exp_{poly} = (N_{As} \times N_{Ps} \times N_{Pe})^{1/3}$$

Where Exp_{poly} is the product of the mean pest damage in each of the predator monocultures: *A. sericeasur* (N_{As}), *P. simplex* (N_{Ps}), and *P. ejectus* (N_{Pe}). To determine if predator polycultures reduced or enhanced pest risk, we subtracted Exp_{poly} from each of the observed pest damage measurements in the predator polyculture (Obs_{poly}) to estimate the deviance (D_{poly}) from the expected null (Exp_{poly}):

$$(2) D_{poly} = Obs_{poly} - Exp_{poly}$$

We calculated D_{poly} for each pest species’ damage in the single-pest and the diverse-pest treatments and used one-sample t-tests or a Wilcoxon Sign test to determine if D_{poly} was significantly negative (enhancement) or positive (reduction). In the diverse pest treatment, we also compared a pest damage index. Finally we compared D_{poly} values in the single-

and diverse-pest treatments with two-sample t-tests or non-parametric Mann-Whitney tests.

To determine if pest diversity affects pest risk to predators, we used a second null model approach. Using the min-max scaled damage values, we then applied a multiplicative risk model for additive experimental designs (Philpott, Pardee & Gonthier 2012). The model estimates an expected amount of pest damage ($Exp_{Div-pest}$) in the diverse-pest treatment given the observed mean values of the *M. ventralis* (N_{Mv}), *H. hampei* (N_{Hh}), and *R. jansonii* (N_{Rj}) single-pest treatments:

$$(3) \quad Exp_{Div-pest} = (N_{Mv} + N_{Hh} + N_{Rj}) - (N_{Mv} \times N_{Hh}) - (N_{Mv} \times N_{Rj}) - (N_{Hh} \times N_{Rj}) + (N_{Mv} \times N_{Hh} \times N_{Rj})$$

We calculated the deviation ($D_{Div-pest}$) of observed pest damage in the diverse-pest treatment ($Obs_{Div-pest}$) from the expected null ($Exp_{Div-pest}$):

$$(4) \quad D_{Div-pest} = Obs_{Div-pest} - Exp_{Div-pest}$$

We calculated $D_{Div-pest}$ values for each of the five predator treatments and used one-sample t-tests to determine if $D_{Div-pest}$ values were significantly negative (enhancement) or positive (reduction). We also compared $D_{Div-pest}$ values for each of the five predator treatments with an Analysis of Variance with a Tukey HSD post hoc test. Tests for normality and statistical analyses were conducted in the Program R (Version 3.1.0).

Results

Ant predator diversity had varying effects on the pest damage (Table 2). In the single-pest treatments, predator diversity had additive effects on pest risk; the observed numbers of leafhoppers (Fig. 1A,E), berries with borers (Fig. 1B,F), and leaf damage by *R. jansoni* (Fig. 1C,G) did not differ from the expected null values. However, in the diverse-pest treatments, predator diversity had synergist negative effects; the observed number of leafhoppers, berries with borers, leaf damage, and combined total pest damage (Fig. 1D,H) were significantly lower than null expectations. Further, the observed number of berries with borers and the amount of leaf damage deviated significantly more from the null expectation in the diverse- relative to the single-pest treatments (Table 2).

Pest diversity significantly reduced pest risk (increased pest damage) by ant predators in all predator treatments with the exception of the predator polyculture (Fig. 2); no ant: $t=4.2, df=19, P=0.0005$; *P. ejectus*: $t=4.8, df=19, P=0.0001$, *P. simplex*: $t=5, df=19, P<0.0001$, *A. sericeasur*: $t=5.5, df=20, P<0.0001$, predator polyculture: $t=0.98, df=19, P=0.3378$. The deviation from the null expectation was significantly larger for all predator treatments relative to the predator polyculture (Fig. 2; $F_{4,96}=3.6, P=0.0089$).

Discussion

Predator diversity enhanced pest risk (increased suppression) to a greater extent in the diverse- relative to the single-pest treatments for berry borer and leaf-chewing beetle pests (Fig. 1B-C,F-G). This increased pest suppression by predator polycultures relative to monocultures may be due to an increased efficiency of predator polycultures or a

decreased efficiency of predator monocultures in the diverse-pest treatment. The analysis of pest diversity effects provides some insight into this question (Fig. 2). Pest diversity reduced suppression in all predator treatments, with the exception of the predator polyculture treatment. Therefore it appears that multiple predator effects were stronger in the diverse pest treatment because pest diversity limited single predator species to a greater extent than predator polycultures.

While pest diversity had a significant impact on the efficiency of multiple predators, the mechanism behind that effect is difficult to clearly separate because pest diversity was manipulated with an additive design. Additive designs confound richness with abundance. For this reasons substitutive designs are ideal for uncovering mechanisms behind biodiversity effects, however substitutive manipulations of pest species that vary in size, weight, and function may make treatments exceedingly unrealistic. For example, while adding 20 berry borers to a treatment replicate may be realistic, adding 20 leaf-chewing beetles to one replicate would exceed any observations of beetle densities in the field. Similarly, if we only added 3 berry borers to a treatment replicate we would be unlikely to observe any berry damage because berry borers have low boring rates. In this study, the question of interest is to understand how pest diversity, including pests of different sizes and functions, impacts predator efficiency therefore it is essential to include variation in pest species form. Thus, we felt it was more important to have a more representative pest community than to attempt to uncover the mechanism behind pest biodiversity effects. For this study, the contributions of pest species richness and pest abundance to the observed change in multiple predator efficiency are therefore unknown.

In other studies, there is evidence that alternative prey species distract predators and increase the searching and/or handling time of prey (Musser & Shelton 2003; Koss & Snyder 2005). However, Wilby and Orwin (2013), Douglass, Duffy & Bruno (2008), and Saleem et al. (2012) found that prey suppression by predator polycultures was weakened by prey richness. While Snyder, Finke & Snyder (2008) showed that predator polycultures always outperformed predator monocultures at suppressing one or two aphid prey species. This variable effect of prey diversity suggests effects might be system specific.

More broadly, many biodiversity experiments that have manipulated foodweb complexity, such as food-chain length or diversity at different or multiple trophic levels, reveal that biodiversity effects on ecosystem function are context dependent (Douglass, Duffy & Bruno 2008; Philpott, Pardee & Gonthier 2012; Wilby & Orwin 2013). These experiments highlight that the effects of biodiversity are not always captured by simple experimental designs, and therefore incorporating more complexity in experiments often uncovers the unpredicted importance of biodiversity. Our results corroborate this notion by showing that prey diversity modifies the efficiency of multiple predators.

This study also highlights the importance of ants as pest control agents in agroecosystems. Indeed ants have played a historic role in agriculture since the recorded history of pest control as an agricultural practice (Van Mele 2008; Offenberg 2015). Ants sometimes increase the density of some hemiptera pest species and for that reason ants are not always considered beneficial organisms (Styrsky & Eubanks 2007). However, in many cases it appears that by reducing the abundance of more damaging pest species, ants that even promote minor pests may have a net positive effect on plants (Eubanks

2001). Our results corroborate the findings of other studies that suggest that greater ant biodiversity improves the suppression of pests (Philpott, Pardee & Gonthier 2012; Wielgoss *et al.* 2014).

Many agroecosystems often maintain complex ecology communities with diverse and dynamic pest assemblages. Indeed, the relative economic importance of different pest species varies drastically in time and space. Our study suggests that in agricultural crops that have multiple pest species of economic importance, practitioners may wish to consider the introduction of pest control strategies that incorporate a diversity of predator species. Further, for practitioners that conserve vegetation features (conservation biological control) to maintain natural populations of predators, practitioners may wish to use multiple methods to ensure the conservation of predator biodiversity.

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References

Altieri, M.A. (1987) *Agroecology*. Westview Press, Inc., Boulder, CO.

- Barrera, J.F., Herrera, J. & Gómez, J. (2008) Fluctuación de la población de adultos de *Rhabdopterus jansonii* (Jacoby) (Coleoptera: Chrysomelidae) en cafetales del Soconusco, Chiapas, Mexico. *Entomología Mexicana*, **7**, 246-251.
- Douglass, J.G., Duffy, J.E. & Bruno, J.F. (2008) Herbivore and predator diversity interactively affect ecosystem properties in an experimental marine community. *Ecology letters*, **11**, 598-608.
- Eubanks, M.D. (2001) Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. *Biological Control*, **21**, 35-43.
- Field, C.B., Behrenfeld, M.J., Randerson, J.T. & Falkowski, P. (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**, 237-240.
- Finke, D.L. & Snyder, W.E. (2008) Niche partitioning increases resource exploitation by diverse communities. *Science*, **321**, 1488-1490.
- Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P.K. (2005) Global consequences of land use. *Science*, **309**, 570-574.
- Gonthier, D., Ennis, K., Philpott, S., Vandermeer, J. & Perfecto, I. (2013) Ants defend coffee from berry borer colonization. *BioControl*, **58**, 815-820.
- Griffen, B.D. (2006) Detecting emergent effects of multiple predator species. *Oecologia*, **148**, 702-709.

- Griffin, J.N., Byrnes, J.E.K. & Cardinale, B.J. (2013) Effects of predator richness on prey suppression: a meta-analysis. *Ecology*, **94**, 2180-2187.
- Jiménez-Soto, E., Cruz-Rodríguez, J.A., Vandermeer, J. & Perfecto, I. (2013) *Hypothenemus hampei* (Coleoptera: Curculionidae) and its interactions with *Azteca instabilis* and *Pheidole synanthropica* (Hymenoptera: Formicidae) in a shade coffee agroecosystem. *Environmental Entomology*, **42**, 915-924.
- Koss, A.M. & Snyder, W.E. (2005) Alternative prey disrupt biocontrol by a guild of generalist predators. *Biological Control*, **32**, 243-251.
- Kremen, C., Iles, A. & Bacon, C. (2012) Diversified farming systems: An agroecological, systems-based alternative to modern industrial agriculture. *Ecology and Society*, **17**, 44.
- Kuesel, R., Gonthier, D., Cruz, M., Vaidya, C., Iverson, A.A. & Perfecto, I. (2014) Local management and landscape use intensity associated with a coffee leaf-chewing beetle. *Agroecology and Sustainable Food Systems*, **38**, 532-540.
- Letourneau, D.K., Jedlicka, J.A., Bothwell, S.G. & Moreno, C.R. (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.
- Musser, F.R. & Shelton, A.M. (2003) Predation of *Ostrinia nubilalis* (Lepidoptera: Crambidae) Eggs in Sweet Corn by Generalist Predators and the Impact of Alternative Foods. *Environmental Entomology*, **32**, 1131-1138.
- Offenberg, J. (2015) REVIEW: Ants as tools in sustainable agriculture. *Journal of Applied Ecology*, **52**, 1197-1205.

- Philpott, S.M., Arendt, W.J., Armbrrecht, I., Bichier, P., Diestch, T.V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., Tejeda-Cruz, C., Williams-Linera, G., Valenzuela, J. & Zolotoff, J.M. (2008) Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. *Conservation Biology*, **22**, 1093-1105.
- Philpott, S.M., Pardee, G.L. & Gonthier, D.J. (2012) Cryptic biodiversity effects: importance of functional redundancy revealed through addition of food web complexity. *Ecology*, **93**, 992-1001.
- Rand, T.A., Tylianakis, J.M. & Tschardtke, T. (2006) Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecology letters*, **9**, 603-614.
- Redak, R.A., Purcell, A.H., Lopes, J.R.S., Blua, M.J., Mizell, R.F. & Andersen, P.C. (2004) The biology of xylem fluid-feeding insect vectors of *Xylella fastidiosa* and their relation to disease epidemiology. *Annual Review of Entomology*, **49**, 243-270.
- Root, R.B. (1973) Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*, **43**, 95-124.
- Saleem, M., Fetzer, I., Dormann, C.F., Harms, H. & Chatzinotas, A. (2012) Predator richness increases the effect of prey diversity on prey yield. *Nature Communications*, **3**, 1305.
- Siemann, E. (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, **79**, 2057-2070.

- Sih, A., Englund, G. & Wooster, D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, **13**, 350-355.
- Snyder, G.B., Finke, D.L. & Snyder, W.E. (2008) Predator biodiversity strengthens aphid suppression across single- and multiple-species prey communities. *Biological Control*, **44**, 52-60.
- Styrsky, J.D. & Eubanks, M.D. (2007) Ecological consequences of interactions between ants and honeydew-producing insects. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 151-164.
- Tirok, K. & Gaedke, U. (2010) Internally driven alternation of functional traits in a multispecies predator-prey system. *Ecology*, **91**, 1748-1762.
- Tylianakis, J.M. & Romo, C.M. (2010) Natural enemy diversity and biological control: Making sense of the context-dependency. *Basic and Applied Ecology*, **11**, 657-668.
- Van Mele, P. (2008) A historical review of research on the weaver ant *Oecophylla* in biological control. *Agricultural and Forest Entomology*, **10**, 13-22.
- Vandermeer, J., Perfecto, I. & Philpott, S. (2010) Ecological complexity and pest control in organic coffee production: uncovering an autonomous ecosystem service. *Bioscience*, **60**, 527-537.
- Wielgoss, A., Tschardtke, T., Rumedé, A., Fiala, B., Seidel, H., Shahabuddin, S. & Clough, Y. (2014) Interaction complexity matters: disentangling services and disservices of ant communities driving yield in tropical agroecosystems. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132144.

- Wilby, A. & Orwin, K.H. (2013) Herbivore species richness, composition and community structure mediate predator richness effects and top-down control of herbivore biomass. *Oecologia*, **172**, 1167-1177.
- Wilby, A. & Thomas, M.B. (2002) Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology letters*, **5**, 353-360.

Table 1. Ant predator and pest treatments and sample size.

Ant species treatments	Pest species treatments			
	leafhopper <i>M. ventralis</i>	berry borer <i>H. hampei</i>	leaf chewer <i>R. jansoni</i>	3 pest spp.
No ants	N=25	N=25	N=29	N=19
<i>A. sericeasur</i>	N=20	N=20	N=20	N=21
<i>P. ejectus</i>	N=20	N=20	N=19	N=20
<i>P. simplex</i>	N=20	N=20	N=20	N=20
3 ant spp.	N=20	N=21	N=20	N=20

Table 2. Statistical comparisons of deviation from null expectations for predator diversity.

	<i>M. ventralis</i>		<i>H. hampei</i>		<i>R. jansoni</i> Wald χ^2	P	3 pest damage index	
	F	P	F	P			F	P
Ant	10.6	<0.001	19	<0.001	14.4	0.001	12.3	<0.001
Herbivore richness	1.7	0.197	0.1	0.71	1.0	0.315	-	-
Ant \times Herb	1.2	0.303	1.2	0.317	4.6	0.102	-	-

Figure captions

Figure 1. Mean (\pm SE) Pest damage across ant predator treatments and the pest treatments for (A) *M. ventralis* leafhoppers, (B) berries bored by *H. hampei*, (C), leaf damage (mm^2) by *R. jansoni*, and (D) combined damage index (sum of the of the min-max scaling of each pest in diverse pest treatment). Deviance (D_{poly}) (\pm SE) from expected null values (Exp_{poly}) for predator diversity effects in single- and diverse-pest treatments for (E) leafhoppers, (F) berries bored, (G) leaf damage (boxplot), and (H) combined pest damage index. Expected null values (Exp_{poly}) were calculated from mean observed pest damage in ant predator monocultures.

Figure 2. Deviance ($D_{Div-herb}$) (\pm SE) from expected values ($Exp_{Div-pest}$) for pest diversity in the five predator treatments. Expected null values ($Exp_{Div-pest}$) were calculated from mean observed pest damage in single pest treatments.

Fig. 1

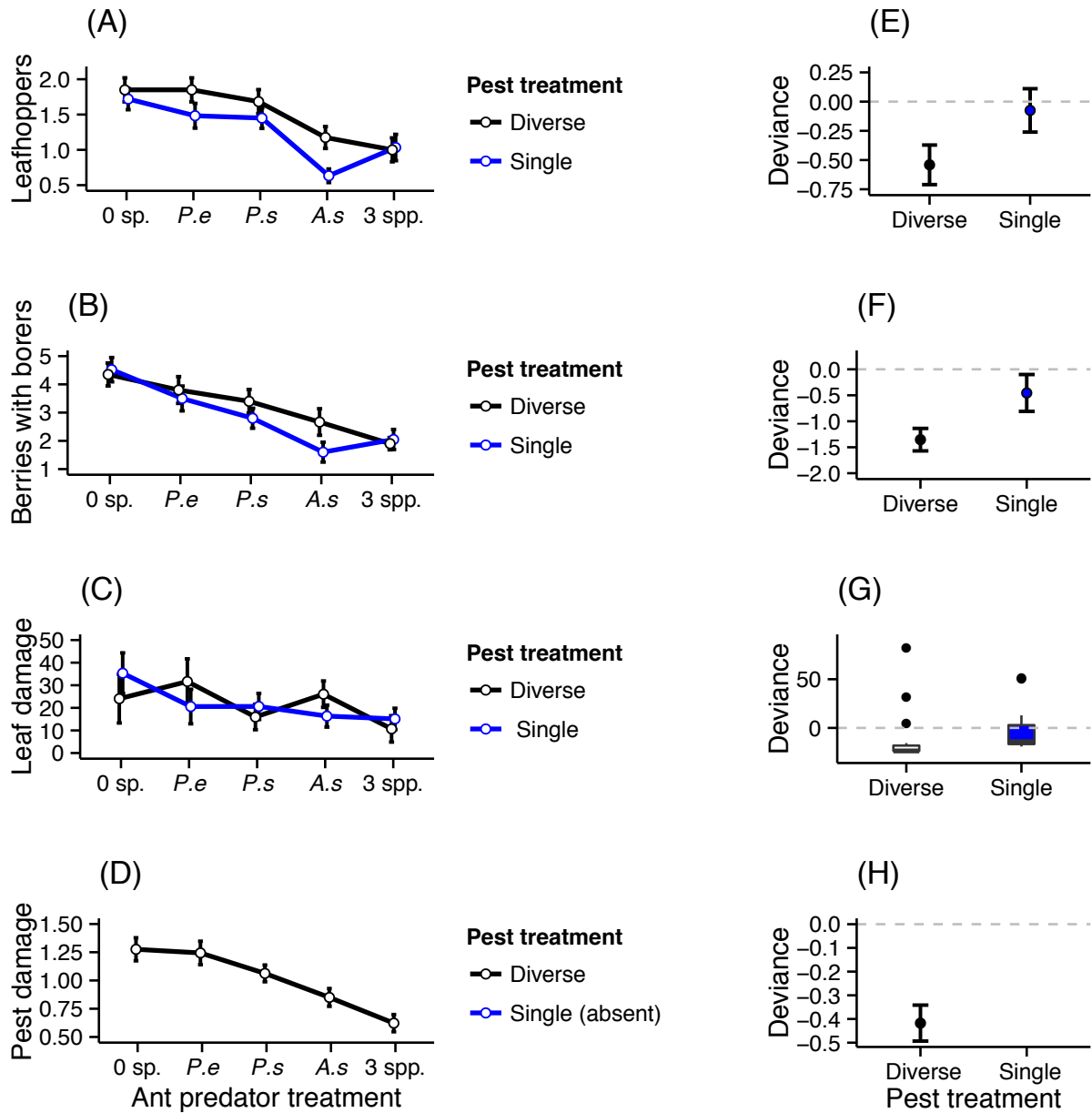


Fig. 2

