

Effects of plant intraspecific diversity across three trophic levels: Underlying mechanisms and plant traits¹

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PREMISE OF STUDY: Although there is increasing recognition of the effects of plant intraspecific diversity on consumers, the mechanisms by which such effects cascade up to higher trophic levels remain elusive.

METHODS: We evaluated the effects of plant (lima bean, *Phaseolus lunatus*) intraspecific diversity on a suite of insect herbivores (leaf-chewers, aphids, and seed-eating beetles) and their third trophic-level associates (parasitoids and aphid-tending ants). We established plots of three plants, classified as monocultures of one population source or polycultures with mixtures of three of the four population sources (N = 16 plots per level of diversity). Within each plot, plants were individually placed in pots and canopy contact was prevented, therefore eliminating diversity effects on consumers arising from changes in plant traits due to plant physical interactions.

KEY RESULTS: Plant diversity reduced damage by leaf-chewers as well as aphid abundance, and the latter effect in turn reduced ant abundance. In contrast, plant diversity increased the abundance of seed-eating beetles, but did not influence their associated parasitoids. There were no effects of diversity on seed traits potentially associated with seed predation, suggesting that differences in early season herbivory between monocultures and polycultures (a likely mechanism of diversity effects on plants since plant interactions were prevented) did not drive concomitant changes in plant traits.

CONCLUSIONS: This study emphasizes that effects of plant intraspecific diversity on consumers are contingent upon differences in associate responses within and among higher trophic levels and suggests possible mechanisms by which such effects propagate up this food web.

KEY WORDS herbivory; lima bean; parasitism; plant intraspecific diversity; plant-mediated effects; tri-trophic interactions

The ecological effects of plant inter- and intraspecific diversity in both managed and natural systems are well documented (reviewed by Hooper et al., 2005; Hughes et al., 2008). Previous studies have found that an increase in both types of plant diversity leads to greater primary productivity (Tilman et al., 1996; Crutsinger et al.,

2006; Moreira et al., 2012), greater stability in functional processes (Naeem et al., 1994; Tilman et al., 2006), as well as greater abundance and diversity of consumers (Siemann, 1998; Haddad et al., 2009; Scherber et al., 2010; Cook-Patton et al., 2011). Plant diversity thus plays a fundamental role in maintaining ecosystem function as well as sustaining diversity at higher trophic levels (Castagneyrol and Jactel, 2012; Moreira et al., 2016a), and is a key feature to consider for ecosystem management and conservation purposes (Parker et al., 2010; Cook-Patton et al., 2011).

Although most of the initial work centered on evaluating the effects of plant species diversity (Hooper et al., 2005), over the last decade there has been growing interest in the effects of plant intraspecific diversity on ecosystem function and associated consumer communities (Hughes et al., 2008). Studies have shown positive effects of plant intraspecific diversity on arthropod diversity and abundance (Crutsinger et al., 2006; Moreira and Mooney, 2013), as well as effects on consumptive interactions such as herbivory and predation (Parker et al., 2010; McArt and Thaler, 2013; Abdala-Roberts and Mooney, 2014). Such effects have been attributed

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mainly to increases in plant growth due to plant-plant interactions (e.g., Crutsinger et al., 2006; Cook-Patton et al., 2011) or greater habitat heterogeneity influencing consumer foraging (see Agrawal et al., 2006; Hambäck et al., 2014). Nonetheless, to date most studies have not tested these different pathways, e.g., explicitly testing for effects of diversity on herbivores or predators via differences in plant biomass or herbivore abundance, respectively (i.e., density-mediated effects; see Abdala-Roberts and Mooney, 2014). As a consequence, we still lack a good understanding of plant diversity effects on consumer recruitment and abundance and how such effects scale-up to influence associated communities (Mooney and Singer, 2012; Staab et al., 2015).

Another important consideration is that, while research on plant functional diversity has gained substantial insight on the traits underlying effects of plant interspecific diversity (Hooper et al., 2005), few studies have assessed the plant traits responsible for plant intraspecific diversity effects on consumers (Moreira et al., 2016a). Indeed, the few studies conducted thus far have found that plant intraspecific diversity effects are mediated by specific plant traits (Hughes, 2014; Moritz et al., 2016), hence the importance of identifying such traits and evaluating their effects on consumers to achieve predictive understanding of these dynamics. Similarly, it is also well recognized that plant species diversity effects on higher trophic levels are contingent upon consumer traits (Bommarco and Banks, 2003; Plath et al., 2012). For example, dietary specialist herbivores are restricted to feeding on a particular plant species or genotype and should thus be negatively influenced by reductions in density of preferred species with increasing diversity (i.e., limited recruitment to high diversity patches which contain a lower density of host plants), whereas generalist herbivores in most cases should be relatively insensitive to such effects as they can switch among host plants regardless of such reduction in density of individual plant species (Root, 1973; Jactel and Brockerhoff, 2007; Abdala-Roberts et al., 2015). Nonetheless, few studies have determined whether such predictions hold for plant intraspecific diversity (but see Castagnyrol et al., 2012).

This study tested the effects of plant (lima bean, *Phaseolus lunatus* L., Fabaceae) intraspecific diversity on insect herbivores and their third trophic-level associates, namely on herbivory by dietary generalist insect leaf-chewers, abundance of generalist aphids, aphid-tending ants, specialist seed-eating beetles, and parasitoids attacking the latter. We eliminated diversity effects on plant biomass arising from plant-plant interactions by preventing above- and belowground physical interactions among neighboring plants, and therefore focused on other mechanisms such as habitat heterogeneity (Abdala-Roberts and Mooney, 2014). In addition, we measured plant reproductive traits (e.g., seed output, seed size, flowering phenology) potentially associated with attack by seed predators and determined if effects of diversity on the third trophic level were mediated by changes in herbivore abundance. We predicted a negative effect of diversity on the specialist seed-eating beetle and a null or positive effect on generalist leaf-chewers and aphids, and that such effects would in turn drive concomitant effects (in the same direction as for the herbivores they recruit to) on species located at the third-trophic level (i.e., ants and parasitoids). Overall, this study builds toward a better understanding of plant diversity effects on associated faunas by providing an assessment of effects on consumers across multiple trophic levels, as well as a detailed inspection of the plant traits and mechanisms by which such effects cascade up through this food web.

MATERIALS AND METHODS

Natural history—Lima bean, *Phaseolus lunatus*, is a self-compatible annual legume distributed along the Pacific coast of Mexico to South America (Freytag and Debouck, 2002; Heil, 2004; Delgado-Salinas et al., 2006). At our field site, located 15 km northwest of Puerto Escondido, Oaxaca, Mexico (15°55'27.4"N, 97°09'03.0"W), lima bean germinates during June and July and flowers at the beginning of October. In addition, seeds are produced during November and December and disperse in January and February (Hernández-Cumplido et al., 2016a, b). Leaves are divided into three oval-shaped leaflets that are arranged alternately on the stem (Freytag and Debouck, 2002).

At our field sites, Lima bean is attacked by several species of insect herbivores which feed on this species early in the growing season, namely the leaf-chewers *Spodoptera eridania* (Stoll) (Lepidoptera: Noctuidae), *Diabrotica balteata* LeConte (Coleoptera: Chrysomelidae), and *Cerotoma ruficornis* Olivier (Coleoptera: Chrysomelidae) (Moreira et al., 2015a; Hernández-Cumplido et al., 2016b). *Spodoptera eridania* is a polyphagous moth native to the neotropics (Capinera, 2001), whereas *Diabrotica balteata* is a polyphagous beetle distributed from North America to Central America; adults of this latter species can severely defoliate adult and young plants (Teng et al., 1984). *Cerotoma ruficornis* specializes on the genus *Phaseolus* and is widely distributed in the neotropics (Kogan and Herzog, 1980). In addition, lima bean is fed upon by the generalist aphid *Aphis gossypii* Glover (Hemiptera: Aphididae) which forms colonies near the tips of new shoots, leaves, and flower buds (Moreira et al., 2016b). Aphids are usually tended by workers of the ant *Solenopsis geminata* Fabricius (Hymenoptera: Formicidae), which feed on the aphid's honeydew (Moreira et al., 2016b; Hernández-Cumplido et al., 2016a). This ant species is found at forest edges or on agricultural crops worldwide (Holway et al., 2002) and readily attacks nonaphid herbivores on lima bean (X. Moreira, personal observation). Finally, mature seeds of lima bean are heavily attacked by species of late-season seed-eating beetles (hereafter "seed predators") belonging to the genera *Acanthoscelides* and *Zabrotes* (Chrysomelidae: Bruchinae) (Campan and Benrey, 2004; Alvarez et al., 2006; Moreira et al., 2015b; Hernández-Cumplido et al., 2016b). During this study, lima bean seeds were attacked almost exclusively by *Acanthoscelides obtectus* Say (approximately 90%), which specializes on the genus *Phaseolus* (Moreira et al., 2015b). At our field site, this beetle is in turn attacked by *Horismenus* spp. and *Stenocorse bruchivora* Crawford parasitic wasps (Hansson et al., 2004; Laurin-Lemay et al., 2013; Moreira et al., 2015b; Hernández-Cumplido et al., 2016b).

The distinction between chewing and sap-feeding herbivores is especially important when assessing plant-mediated effects among herbivores. Phloem-sucking/piercing herbivores (e.g., aphids) commonly induce the salicylic acid defense pathway whereas leaf chewing herbivores (e.g., caterpillars and beetles) typically induce the jasmonic acid pathway (Thaler et al., 2012). Accordingly, feeding by one herbivore guild might induce resistance to future attack by the same guild, but might increase susceptibility to the other guild due to interference between plant defense signaling pathways (Rodríguez-Saona et al., 2005). Having said this, early season herbivory in our system is caused by both chewing and sap-feeding species which makes it difficult to predict the directionality of effects on late season seed herbivores.

Experimental set-up and measurements—In early October 2013, we collected seed pods from five to ten wild *Phaseolus lunatus* plants from each of four populations along the Pacific coast of Oaxaca, Mexico (distance among populations ranged from 50 to 160 km; for further details see Moreira et al., 2016b), and transported them to the laboratory where they were refrigerated. Seeds with any type of damage were discarded. Results from one-way general linear models indicated that the sampled populations varied significantly in: (1) reproductive output (pod number: 2-fold, $F_{3,46} = 60.24$, $P < 0.0001$); (2) growth (leaf production: 1.5-fold, $F_{3,58} = 82.66$, $P < 0.0001$); (3) seed traits (e.g., protein content g/100 g d.w.: 1.7-fold, $F_{3,42} = 3.26$, $P = 0.031$); and (4) insect abundance (seed predators: 2.4-fold, $F_{3,46} = 13.63$, $P < 0.0001$; aphids: $F_{3,58} = 63.72$, $P < 0.0001$). On 15 November 2014, we individually sowed seeds in 5-L pots with a mixture of native soil and peat moss. Upon seedling emergence, we kept plants for four weeks in herbivore-free nylon mesh field cages (Outdoor Cage 6' × 6' × 6', 20 × 20 Mesh Lumite from Bioquip Products, Rancho Dominguez, California, USA) under homogeneous growing conditions. This approach was aimed at reducing (though does not entirely eliminate) maternal effects (Abdala-Roberts and Mooney, 2013). After four weeks, on 15 December 2014, we transferred plants to the experimental field site (Universidad del Mar, Puerto Escondido Campus, Oaxaca, México: 15°55'26.4"N, 97°09'02.0"W) and randomly allocated them to plots of three plants each. Plots were classified as either monocultures of one population source ($N = 16$, four per population) or polycultures composed of mixtures of three out of the four populations ($N = 16$). Population mixtures were composed of randomly selected populations, and each population was present in a similar number of polyculture plots (11 or 12). Because we sampled different populations rather than genotypes within a population, the experiment addressed the effects of population-level intraspecific diversity on higher trophic levels. Admittedly, growing different populations or genotypes from different populations within a single common garden may lead to an overestimation of plant intraspecific effects on consumers (Tack et al., 2012). However, we note that *P. lunatus* population variation in vegetative (e.g., leaf production) and reproductive (e.g., pod number) traits in this study ranged from 1.5 to 2.0 fold, respectively which is only slightly greater than the magnitude of variation among genotypes within previously sampled wild populations of this species (Ballhorn et al., 2011). Therefore, we argue that the magnitude of trait variation evaluated in this study is relevant for understanding the ecological effects of intraspecific variation occurring at a local (site-level) scale in this species.

Within each plot, potted plants were separated by 20 cm and their canopies were prevented from touching by tying the main stem to a wooden stick planted in the soil; distance between adjacent plots was 1.5 m. These methodological features were aimed at eliminating belowground and aboveground physical interactions (though not airborne volatile communication) among neighboring plants and thus precluded effects of diversity on plant traits and biomass due to plant-plant physical interactions (Abdala-Roberts and Mooney, 2014). Based on these experimental features and considering that previous work has shown strong effects of early-on late-season herbivores in lima bean (Hernández-Cumplido et al., 2016b), differences in early season herbivory represent a possible cause for diversity effects on plant traits, which in turn are predicted to influence late-season seed predators (i.e., a diversity-mediated indirect effect among herbivore guilds).

We conducted two surveys of leaf herbivory, aphid abundance, and ant abundance: one of each on 28 January 2015 and 11 February 2015 (plants had flowers and green pods during the latter date). Surveys of aphids and ants involved a careful examination of all stems and leaves per plant. To estimate leaf herbivory, we counted the number of damaged and undamaged leaflets, and used the proportion of damaged leaflets for statistical analyses. This method provided a reliable estimate of the magnitude of herbivory because amounts of leaf area lost were fairly consistent (ca. 25%) among leaflets (X. Moreira, personal observation); although this method overestimates the actual amount of total leaf area consumed per plant, this effect was consistent across all plants and thus did not introduce a bias in the results. We did not estimate leaf damage separately for each leaf chewer species because in many cases it was not possible to discriminate damage by each one, particularly between *Ceratomyza ruficornis* and *Diabrotica balteata*. For each plant, we also recorded if flowering initiated during the first or second half of February as a measure of flowering onset, and analyzed the proportion of plants flowering the first half of February per plot. In addition, at the end of the growing season (early March 2015), once plants started wilting, we harvested all mature bean pods per plant every other day until senescence. We shelled the pods, counted the number of seeds, and used a subsample of five randomly chosen seeds per plant to measure seed size (length, in mm) and quantify protein content (g/100 g d.w.). Protein content was quantified using the Bradford assay (Bradford, 1976) and expressed as g/100 g of d.w. (for details see Hernández-Cumplido et al., 2016b). Seeds of each plant were individually placed in ventilated plastic containers and incubated under controlled conditions (26°C day temperature, 14 h daylight, 70% r.h.). We inspected each container daily to record seed predator and parasitoid emergence. We also recorded the number of seed predators and the number seeds attacked by these herbivores by visual inspection and used the proportion of attacked seeds for statistical analyses.

Statistical analyses—*Diversity effects on insect abundance and herbivory*—We ran plot-level generalized linear models testing for the effects of plant intraspecific diversity (fixed) on leaf herbivory, abundance of aphids, ants, seed predators, and parasitoids, and the proportion of attacked seeds. For leaf herbivory, we performed a repeated-measures model that also included the effect of survey and the diversity × survey interaction as we found temporal (between-survey) variation in diversity effects (see Results). In contrast, for ant and aphid abundance, both of which were also surveyed on two different dates, we used mean values across surveys as there was no evidence of temporal variation in diversity effects in either case (nonsignificant diversity × survey interaction: $\chi^2_{1,30} = 2.23$, $P = 0.135$ and $\chi^2_{1,30} = 1.11$, $P = 0.291$, respectively).

Diversity effects on plant traits and effects on late-season seed predators—We tested for effects of diversity on seed number, seed size (mean and CV), seed protein content (g/100 g d.w., mean and CV), and flowering onset (proportion of plants flowering the first half of February). In addition, we reran the model for seed predator abundance (above) including as covariates all the measured plant reproductive traits. If one or more traits strongly mediate the effect of diversity on herbivores, then an effect of diversity on seed predators (from the original model not including traits) should turn nonsignificant once the trait(s) is(are) accounted for. Alternatively, if the effect of diversity remains significant after including plant traits

this would mean either that these traits do not mediate the diversity effect or that they are important to a certain degree but do not fully explain such effect. We chose seed size because it is a proxy of seed quality for seed predators (Herrera, 2000) and is positively correlated with seed predator attack in lima bean (Hernández-Cumplido et al., 2016b) as well as other species of *Phaseolus* (Benrey et al., 1998; Campan and Benrey, 2006; Zaugg et al., 2013; Moreira et al., 2015b). Similarly, we analyzed differences in seed protein content (g/100 g d.w.) because this trait is correlated with seed quality for seed predators and has also been shown to influence seed predator attack in lima bean (Hernández-Cumplido et al., 2016b). In addition, we also analyzed differences in the coefficient of variation (CV) in seed size and protein content as previous work has shown that variability in seed traits can influence seed predator attack (e.g., CV in seed size; Shimada et al., 2015). We also used seed number because it represents a measure of resource availability expected to influence seed predator recruitment. Finally, we chose flowering onset because previous work suggests that early season herbivory leads to earlier flowering in lima bean which in turn leads to escape from seed predators (Hernández-Cumplido et al., 2016b).

Mechanisms of diversity effects on ants and parasitoids—To test for mechanisms of effects on higher trophic levels, whenever the diversity effect on ant or parasitoid abundance was significant we ran these models again including aphid abundance or seed predator abundance as covariates (respectively), as well as the aphid abundance or parasitoid abundance \times diversity interaction. If diversity effects on the third trophic level are mediated by herbivore abundance (i.e., a density-mediated indirect effect or “interaction chain”; sensu Wootton, 1994), then significant diversity effects on ants and parasitoids should become nonsignificant once aphid or seed predator abundance are accounted for, respectively. If a diversity effect remains significant, this suggests effects occurring independently of differences in herbivore abundance (e.g., changes in consumer traits influencing herbivore-ant or herbivore-parasitoid interactions; Abdala-Roberts and Mooney, 2013).

General considerations—Whenever residuals were not normally distributed, we used generalized linear models as a more powerful alternative to data transformations (Bolker et al., 2009). The only exceptions were seed protein content and the proportion of plants flowering early, which were normally distributed. For seed size and CV of seed size we used a gamma distribution (log link), which handles continuous data with different types of nonnormal distributions (Zuur et al., 2009). For leaf herbivory and seed attack (proportions, no evidence of overdispersion) we used a binomial distribution (logit link), whereas seed number and aphid abundance were overdispersed so we used a negative binomial distribution (log link) which accounts for this condition (Bolker et al., 2009). For seed predator, ant, and parasitoid abundance we used a Poisson distribution (log link), as there was no evidence of overdispersion. All analyses were conducted with PROC GLIMMIX in SAS version 9.2 (SAS, 2008), using plot-level means, and we report least-square means and standard errors as descriptive statistics.

Test of nonadditivity of diversity effects—Whenever a diversity effect on insects was significant in the above models, we determined if such effect was additive, e.g., due to the presence of one or more resistant or susceptible genotypes (populations in our case) in

mixtures (“sampling” effect; Houston, 1997), or nonadditive where polycultures exhibit higher or lower insect abundance as a consequence of emergent, patch-level properties resulting from interactive effects among genotypes (Johnson et al., 2006). Following Johnson et al. (2006), we calculated lima bean population means for each variable at low diversity (i.e., expected values), and compared these values to the mean of each population at high diversity (i.e., observed values). For each response variable, we compared observed and expected values with a one-way general linear model using PROC MIXED in SAS version 9.2. These models also included the effects of plot (i.e., group of three plants) and population nested within plot, making them similar to a paired test comparing observed vs. expected values for each population source. A significant difference between observed and expected values is necessarily due to nonadditivity as the comparison is performed by specifying the monoculture values of each population (i.e., sampling effects are accounted for by including population-specific expected values).

RESULTS

Effects of diversity on leaf-chewers and aphids—We found a significant negative effect of plant diversity on leaf damage (Table 1), where polycultures exhibited a 42% lower proportion of damaged leaves (0.11 ± 0.004) relative to monocultures (0.19 ± 0.01) (Fig. 1A). Subsidiary analyses indicated that this effect was nonadditive ($F_{1,46} = 168.05$, $P < 0.0001$). In addition, we found a significant diversity \times survey date interaction (Table 1) where the effect of

TABLE 1. Effects of lima bean (*Phaseolus lunatus*) population-level intraspecific diversity on herbivory by insect leaf-chewers (*Spodoptera eridiana*, *Diabrotica balteata*, and *Ceratoma ruficornis*), abundance of aphids (*Aphis gossypii*), abundance of seed predators (mostly *Acanthoscelides obtectus*), abundance of parasitoids (several species) attacking seed predators, abundance of aphid-tending ants (*Solenopsis geminata*), the proportion of seeds attacked by seed predators, plant growth (leaf number), reproductive output (seed number), seed size (mm) and protein content (g/100 g d.w.), and flowering onset (proportion of plants that flowered early). *F*- or χ^2 values (the latter for binomial and Poisson models) and *P*-values (in parenthesis) are shown. The herbivory model included the effects of survey ($\chi^2_{1,30} = 3.44$, $P = 0.063$), and the diversity \times survey interaction ($\chi^2_{1,30} = 16.38$, $P < 0.0001$). In all cases, degrees of freedom ranged from 1, 28 to 1, 30. Significant ($P < 0.05$) and marginally significant ($0.05 < P < 0.10$) effects are in bold and italics, respectively. E = early season herbivore, L = late season herbivore.

| Response variable | Diversity effect |
|-----------------------------|--------------------------|
| <i>Herbivores</i> | |
| Leaf damage (E) | 46.26 (<0.001) |
| Aphid abundance (E) | 4.18 (0.049) |
| Seed predator abundance (L) | 6.09 (0.013) |
| Seed attack (L) | 0.07 (0.793) |
| <i>Third trophic level</i> | |
| Ant abundance | 3.57 (0.068) |
| Parasitoid abundance | 0.01 (0.916) |
| <i>Plant traits</i> | |
| Leaf number | 0.04 (0.845) |
| Seed number | 0.66 (0.421) |
| Seed size | 1.82 (0.187) |
| CV seed size | 0.93 (0.341) |
| Seed protein content | 0.37 (0.548) |
| CV seed protein content | 1.39 (0.248) |
| Flowering onset | 1.66 (0.208) |

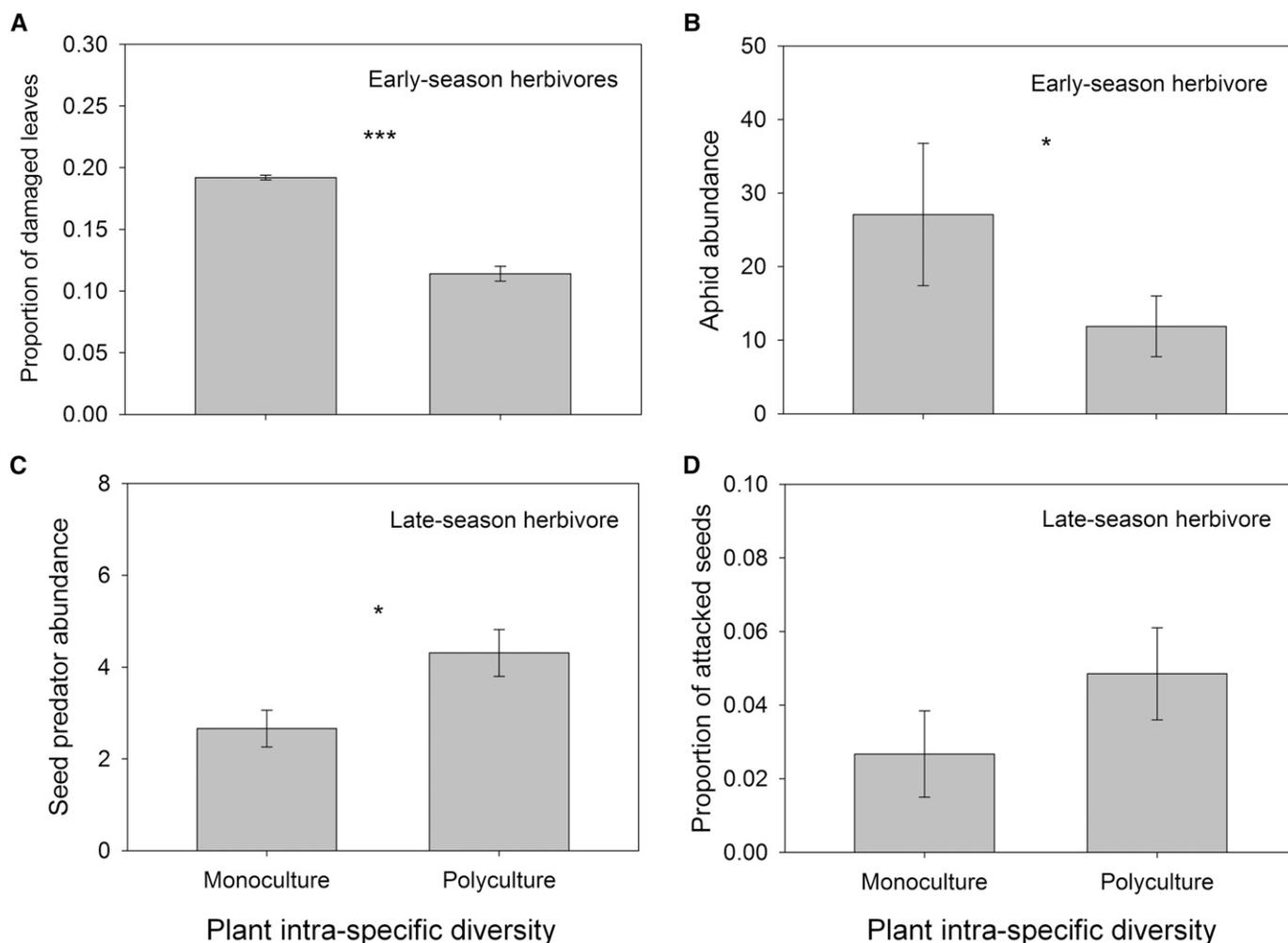


FIGURE 1 Least-square means (\pm SE) for the effects of lima bean (*Phaseolus lunatus*) population-level intraspecific diversity on: (A) herbivory by early season insect leaf-chewers (*Spodoptera eridiana*, *Diabrotica balteata*, and *Ceratoma ruficornis*); (B) abundance of early season aphids (*Aphis gossypii*); (C) abundance of late-season seed predators (*Acanthoscelides obtectus*); and (D) the proportion of seeds attacked by seed predators. * $P < 0.05$, *** $P < 0.0001$.

diversity was stronger during the second survey (55% reduction in mixtures relative to monoculture, i.e., polyculture = 0.09 ± 0.02 , monoculture = 0.20 ± 0.009) than during the first survey (28% reduction in mixtures: polyculture = 0.13 ± 0.009 , monoculture = 0.18 ± 0.009). Similarly, we also found a significant negative effect of plant diversity on aphid abundance (Table 1), where polycultures exhibited a 56% lower mean value (11.88 ± 4.13 aphids) relative to monocultures (27.08 ± 9.67 aphids) (Fig. 1B). This diversity effect on aphids was also nonadditive ($F_{1,46} = 10.19$, $P = 0.003$).

Diversity effects on plant reproductive traits—There were no significant effects of plant diversity on seed number, seed size, CV of seed size, seed protein content, CV of protein content, or flowering onset (Table 1; Appendix S1, see Supplemental Data with the online version of this article).

Diversity effects on seed predators—In contrast to leaf-chewers and aphids, we found a significant positive effect of plant diversity on seed predator abundance (Table 1), where polycultures exhibited a 62% greater mean value (4.31 ± 0.51 seed predators) relative

to monocultures (2.66 ± 0.40 seed predators) (Fig. 1C). Further analyses indicated that this effect was nonadditive ($F_{1,37} = 9.30$, $P = 0.004$). In addition, the effect of diversity on seed predator abundance remained significant after accounting for plant traits (Table 2), suggesting that the selected traits did not fully explain diversity effects on these late-season herbivores. Two of these traits (CV of seed

TABLE 2. Effects of lima bean (*Phaseolus lunatus*) population-level intraspecific diversity on the abundance of the late-season seed-eating beetle *Acanthoscelides obtectus*. The model used a Poisson distribution with log link function. Shown are χ^2 values for the effect of diversity as well as plant traits included as covariates. Significant effects ($P < 0.05$) are in bold. Signs in parentheses indicate direction of effect of plant trait on seed predator abundance.

| Predictor | DF | χ^2 | P-value |
|--------------------------|------|----------|-------------------|
| Diversity | 1,21 | 9.71 | 0.002 |
| Seed size (-) | 1,21 | 0.69 | 0.405 |
| CV seed size (-) | 1,21 | 6.26 | 0.012 |
| Seed protein content (-) | 1,21 | 0.15 | 0.694 |
| CV seed proteins (-) | 1,21 | 0.15 | 0.700 |
| Flowering onset (+) | 1,21 | 21.77 | <0.0001 |

size and flowering onset) were nonetheless significantly associated with seed predator abundance (Table 2). Finally, although polycultures tended to have a greater proportion of attacked seeds, diversity did not significantly influence this variable (Table 1; Fig. 1D).

Diversity effects on ants and parasitoids—There was a marginally significant negative effect of diversity on ant abundance (Table 1), with polycultures exhibiting a 49% lower mean value (8.63 ± 1.79 ants) relative to monocultures (16.78 ± 4.59 ants) (Fig. 2A). After accounting for aphid abundance, the effect of diversity on ants became nonsignificant ($\chi^2_{1,29} = 0.78$, $P = 0.377$), indicating that diversity effects on ants were mediated by the increase in aphid abundance in population mixtures (i.e., density-mediated indirect effect). In contrast, there was no effect of diversity on abundance of parasitoids attacking seed predators (Table 1; Fig. 2B).

DISCUSSION

Intraspecific diversity in lima bean exerted contrasting effects on early season and late-season herbivores. Contrary to theory which predicts null or positive effects of plant diversity on

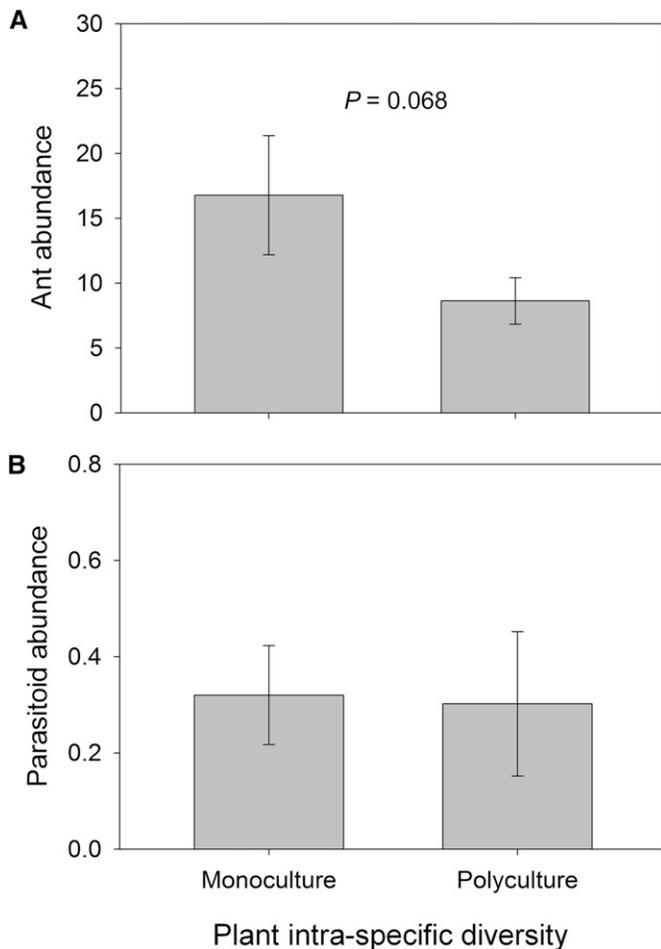


FIGURE 2 Least-square means (\pm SE) for the effects of lima bean (*Phaseolus lunatus*) intraspecific diversity on the abundance of (A) aphid-tending ants (*Solenopsis geminata*) and (B) parasitoids attacking *Acanthoscelides obtectus* seed predators.

dietary generalist herbivores, lima bean diversity negatively influenced the abundance and damage by early season generalist aphids and leaf-chewers, and effects on aphids in turn cascaded-up to negatively influence aphid-tending ants. In contrast, and also contrary to the prediction of negative effects of plant diversity on specialist herbivores, lima bean diversity had a positive effect on the abundance of late-season specialist seed predators but did not influence their parasitoids. These findings highlight the context-dependency of plant diversity effects on associated faunas, where such effects varied both within and across trophic levels depending on consumer identity.

Theory predicts neutral or even positive (e.g., via diet mixing) effects of plant diversity on dietary generalist herbivores as these are not restricted to feeding on a particular plant species or genotype and should thus be insensitive to reductions in density or conspicuity of preferred species or genotypes with increasing diversity (Jactel and Brockerhoff, 2007; Castagneyrol et al., 2012). However, we found negative effects of plant intraspecific diversity on recruitment by the generalist aphid *Aphis gossypii*, as well as on damage caused by three species of leaf-chewers, two of which are generalists (*Spodoptera eridiana* and *Diabrotica balteata*) and caused most of the leaf damage recorded on lima bean during the experiment (X. Moreira, personal observation). These findings suggest that diversity produced some type of chemical or physical interference (e.g., masking of preferred genotypes by other less preferred ones; Denno et al., 2005) which drove a reduction in recruitment to and damage in mixtures by these herbivores (Jactel et al., 2011; Muiruri and Koricheva, 2016). Based on this, we argue that diet breadth may not always be a reliable predictor of the strength or direction of plant diversity effects on herbivores, thus emphasizing the importance of considering other consumer traits (e.g., dispersal, feeding mode) producing herbivore species-to-species contingency in responses to plant diversity (Plath et al., 2012).

Counter to empirical work showing that plant diversity usually reduces damage by dietary specialist insect herbivores (Jactel and Brockerhoff, 2007), we found positive effects of plant intraspecific diversity on the specialist seed predator *Acanthoscelides obtectus*. One plausible mechanism for this result could have been plant phenotypic changes driven by previous patterns of damage by early season herbivores; we speculate lowered recruitment and damage by early season leaf-chewers and aphids in mixtures drove a change in plant traits in polyculture relative to monoculture, and such effects in turn conditioned responses to diversity by late-season seed predators. Although none of the traits measured (i.e., flowering onset, seed size and protein content) differed between monocultures and mixtures, we speculate that changes in other unmeasured traits or cues associated with seed quality (e.g., cyanogenic compounds (Hernández-Cumplido et al., 2016b) or phenolics (Moreira et al., 2015b)) or some other aspect of reproduction could have mediated such effects. Recent work in this system by our group has shown that lima bean plants exposed to early season herbivory are less attacked by late-season seed predators, presumably via changes in seed traits or reproductive phenology (Hernández-Cumplido et al., 2016b). Alternatively, it is also possible that adult female beetles were able to perceive (chemically or visually) higher loads of early season herbivores present in monoculture and thus preferentially oviposited in mixtures to avoid intraspecific competition. However, after accounting for the amount of early season leaf damage and aphid abundance (presumably correlated with chemical and visual cues used by female beetles), the effect of diversity on seed

predator abundance remained significant (results not shown), suggesting that indirect effects via changes in plant traits induced by leafchewers (rather than direct effects of cues) were responsible for the observed pattern. In agreement with this interpretation, a recent study by Muiruri et al. (2015) found that browsing by moose on birch altered effects of tree species diversity on damage by insect herbivores. Because plant species are frequently attacked sequentially by multiple herbivore species, and given the prevalence of plant-mediated interactions via induced responses to herbivory (Van Zandt and Agrawal, 2004; Ohgushi, 2005; Utsumi et al., 2013), this phenomenon could represent a widespread (but currently ignored) mechanism by which plant diversity influences associated consumers.

Although our findings are suggestive of plant diversity-mediated indirect effects of early- on late-season herbivores, we cannot discard other independent dynamics potentially underlying diversity effects on seed predators. For instance, seed predator performance may have been greater in population mixtures because of benefits (e.g., nutrient complementarity or toxin dilution) from switching among host plants of different populations (Mody et al., 2007; Kotowska et al., 2010). In this system, however, diet mixing is unlikely since individuals of *Acanthoscelides obtectus* do not move among seed pods within a plant or among plants. Alternatively, seed predators may have perceived population mixtures differently than monocultures (Rodríguez-Saona et al., 2005) through some plant trait or habitat feature not associated with plant-phenotypic changes due to early season herbivory. For instance, higher seed predator recruitment to mixtures could have been driven by specific volatile blends produced by neighboring plants of different population sources or genotypes (Ninkovic et al., 2011), independently of differences in early season damage. Relatedly, previous work has reported plant-plant airborne communication in lima bean (Heil and Silva Bueno, 2007; Moreira et al., 2016b), which argues for further research to determine the contribution of this phenomenon to explaining diversity effects on herbivore patch selection.

It is important to emphasize that the observed effects of plant intraspecific diversity on leaf and seed herbivory may have particularly important evolutionary implications for annual plant species such as lima bean. In particular, although increased seed predator abundance in polyculture did not lead to greater seed predation (though there was tendency in this direction), we might expect instances where changes in seed predator recruitment influence rates of seed predation and thus shape plant lifetime fitness. Therefore, any effects of diversity on such interactions may lead to rapid evolutionary changes in plant traits mediating interactions with these herbivores, including feedbacks where diversity-mediated changes in herbivore selection in turn influence plant intraspecific diversity within populations (Bailey et al., 2014; Abdala-Roberts and Mooney, 2014). Having said this, additional research using molecular markers is needed first to assess actual levels of genetic diversity within and among lima bean populations and in this way inform future studies manipulating intraspecific diversity in this plant species and track its causes and consequences in a more precise manner (Hughes et al., 2008).

Finally, the effect of plant intraspecific diversity on herbivores cascaded-up to the third trophic level in some (but not all) cases. Specifically, we found that reduced aphid abundance in population mixtures in turn led to lower abundance of aphid-tending ants (i.e., a density-mediated indirect effect; Mooney and Singer, 2012).

Similarly, Moreira and Mooney (2013) found that effects of genotypic diversity in the shrub *Baccharis salicifolia* (Ruiz & Pav.) Pers. on ant abundance were mediated by effects on aphid abundance (though in this study diversity effects on these consumers were positive). In addition, and in contrast to effects on aphids and ants, positive effects of plant diversity on seed predators did not lead to higher parasitoid abundance in mixtures. Together, these findings indicate that bottom-up effects of plant diversity vary among species belonging to the third trophic level and such variation may respond to differences in the mechanisms or nature of interactions between these species and their associated prey or mutualists.

CONCLUSIONS

Although there is a considerable amount of studies addressing effects of plant diversity on consumers, research thus far has been slow at addressing the dynamic complexity and mechanisms underpinning such effects, particularly for research on plant intraspecific diversity. First, future progress, particularly at the intraspecific level, will rely on research identifying (and manipulating diversity in) target plant and consumer traits driving the observed dynamics (Hughes, 2014). Second, a consideration of ecological feedbacks between plant diversity bottom-up effects and consumer top-down effects is also of central importance. Such feedbacks may also have evolutionary implications under the context of plant intraspecific diversity effects if alteration in consumer recruitment or behavior leads to changes in consumer selection on plant traits (Abdala-Roberts and Mooney, 2014). Finally, although our results are not definitive, they are suggestive that plant-mediated indirect interactions are likely a key aspect to consider in future work addressing the effects of producer diversity on plant-centered faunas (Muiruri et al., 2015). To this end, systems where herbivore species exhibit contrasting phenologies offer an ideal opportunity to address plant diversity-mediated interactions among consumers, priority effects, and diversity-initiated feedbacks within and among trophic levels.

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LITERATURE CITED

- Abdala-Roberts, L., and K. A. Mooney. 2013. Environmental and plant genetic effects on tri-trophic interactions. *Oikos* 122: 1157–1166.
- Abdala-Roberts, L., and K. A. Mooney. 2014. Ecological and evolutionary consequences of plant genotype diversity in a tri-trophic system. *Ecology* 95: 2879–2893.

- Abdala-Roberts, L., K. A. Mooney, T. Quijano-Medina, M. J. Campos-Navarrete, A. González-Moreno, and V. Parra-Tabla. 2015. Comparison of tree genotypic diversity and species diversity effects on different guilds of insect herbivores. *Oikos* 124: 1527–1535.
- Agrawal, A. A., J. A. Lau, and P. A. Hambäck. 2006. Community heterogeneity and the evolution of interactions between plants and insect herbivores. *Quarterly Review of Biology* 81: 349–376.
- Alvarez, N., L. Mercier, M. Hossaert-McKey, J. Contreras-Garduño, G. Kunstler, A. Aebi, and B. Benrey. 2006. Ecological distribution and niche segregation of two sibling species of bean beetles, *Acanthoscelides obtectus* Say and *A. obvelatus* Bridwell. *Ecological Entomology* 31: 582–590.
- Bailey, J. K., M. A. Genung, I. Ware, M. Van Nuland, H. Long, and J. A. Schweitzer. 2014. Indirect genetic effects: An evolutionary mechanism linking feedbacks, genotypic diversity, and coadaptation along environmental gradients. *Functional Ecology* 28: 87–95.
- Ballhorn, D. J., S. Kautz, M. Jensen, I. Schmitt, M. Heil, and A. Hegeman. 2011. Genetic and environmental effects on plant defences against herbivores. *Journal of Ecology* 99: 313–326.
- Benrey, B., A. Callejas, L. Rios, K. Oyama, and R. F. Denno. 1998. The effects of domestication of *Brassica* and *Phaseolus* on the interaction between phytophagous insects and parasitoids. *Biological Control* 11: 130–140.
- Bolker, B., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. Henry, and J.-S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution* 24: 127–135.
- Bommarco, R., and J. E. Banks. 2003. Scale as modifier in vegetation diversity experiments: Effects on herbivores and predators. *Oikos* 102: 440–448.
- Bradford, M. M. 1976. A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry* 72: 248–254.
- Campan, E., and B. Benrey. 2004. Behavior and performance of a specialist and a generalist parasitoid of bruchids on wild and cultivated beans. *Biological Control* 30: 220–228.
- Campan, E. and B. Benrey. 2006. Effects of seed type and bruchid genotype on the performance and oviposition behavior of *Zabrotes subfasciatus* (Coleoptera: Bruchidae). *Insect Science* 13: 309–318.
- Capinera, J. L. 2001. Handbook of vegetable pests. Academic Press, San Diego, California, USA.
- Castagneyrol, B., and H. Jactel. 2012. Unravelling plant-animal diversity relationships: A meta-regression analysis. *Ecology* 93: 2115–2124.
- Castagneyrol, B., L. Lagache, B. Biffard, A. Kremer, and H. Jactel. 2012. Genetic diversity increases insect herbivory on oak saplings. *PLoS One* 7: e42427.
- Cook-Patton, S. C., S. H. McArt, A. L. Parachnowitsch, J. S. Thaler, and A. A. Agrawal. 2011. A direct comparison of the consequences of plant genotypic and species diversity on communities and ecosystem function. *Ecology* 92: 915–923.
- Crutsinger, G. M., M. D. Collins, J. A. Fordyce, Z. Gompert, C. C. Nice, and N. J. Sanders. 2006. Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science* 313: 966–968.
- Delgado-Salinas, A., A. R. Bibler, and M. Lavin. 2006. Phylogeny of the genus *Phaseolus* (Leguminosae): A recent diversification in an ancient landscape. *Systematic Botany* 31: 779–791.
- Denno, R. F., D. L. Finke, and G. A. Langellotto. 2005. Direct and Indirect effects of vegetation structure and habitat complexity on predator-prey and predator-predator interactions. In P. Barbosa, and I. Castellanos [eds.], *Ecology of predator-prey interactions*, 211–239. Oxford University Press, New York, New York, USA.
- Freytag, G. F., and D. G. Debouck. 2002. Taxonomy, distribution and ecology of the genus *Phaseolus* (Leguminosae-Papilionoideae) in North America, Mexico and Central America. BRIT Press, Fort Worth, Texas, USA.
- Haddad, N., M. N. Crutsinger, K. Gross, J. Haarstad, J. M. Knops, and D. Tilman. 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. *Ecology Letters* 12: 1029–1039.
- Hambäck, P. A., B. D. Inouye, P. Andersson, and N. Underwood. 2014. Effects of plant neighborhoods on plant-herbivore interactions: Resource dilution and associational effects. *Ecology* 95: 1370–1383.
- Hansson, C., A. Aebi, and B. Benrey. 2004. *Horismenus* species (Hymenoptera: Eulophidae) in a bruchid beetle parasitoid guild, including the description of a new species. *Zootaxa* 548: 1–16.
- Heil, M. 2004. Induction of two indirect defences benefits Lima bean (*Phaseolus lunatus*, Fabaceae) in nature. *Journal of Ecology* 92: 527–536.
- Heil, M., and J. C. Silva Bueno. 2007. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defence in nature. *Proceedings of the National Academy of Sciences, USA* 104: 5467–5472.
- Hernández-Cumplido, J., B. Forter, X. Moreira, M. Heil, and B. Benrey. 2016a. Induced floral and extrafloral nectar production affect ant-pollinator interactions and plant fitness. *Biotropica* 48: 342–348.
- Hernández-Cumplido, J., G. Glauser, and B. Benrey. 2016b. Cascading effects of early-season herbivory on late-season herbivores and their parasitoids. *Ecology* 97: 1283–1297.
- Herrera, C. M. 2000. Measuring the effects of pollinators and herbivores: Evidence for non-additivity in a perennial herb. *Ecology* 81: 2170–2176.
- Holway, D. A., A. V. Suarez, and T. J. Case. 2002. Role of abiotic factors in governing susceptibility to invasion: A test with Argentine ants. *Ecology* 83: 1610–1619.
- Hooper, D. U., F. S. Chapin III, J. J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J. H. Lawton, et al. 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs* 75: 3–35.
- Houston, M. A. 1997. Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia* 110: 449–460.
- Hughes, A. R. 2014. Genotypic diversity and trait variance interact to affect marsh plant performance. *Journal of Ecology* 102: 651–658.
- Hughes, A. R., B. D. Inouye, M. T. Johnson, N. Underwood, and M. Vellend. 2008. Ecological consequences of genetic diversity. *Ecology Letters* 11: 609–623.
- Jactel, H., G. Birgersson, S. Andersson, and F. Schlyter. 2011. Non-host volatiles mediate associational resistance to the pine processionary moth. *Oecologia* 166: 703–711.
- Jactel, H., and E. G. Brockerhoff. 2007. Tree diversity reduces herbivory by forest insects. *Ecology Letters* 10: 835–848.
- Johnson, M. T., M. J. Lajeunesse, and A. A. Agrawal. 2006. Additive and interactive effects of plant genotypic diversity on arthropod communities and plant fitness. *Ecology Letters* 9: 23–34.
- Kogan, M., and D. C. Herzog. 1980. Sampling methods in soybean entomology. Springer-Verlag, New York, New York, USA.
- Kotowska, A. M., J. F. Cahill, and B. A. Keddie. 2010. Plant genetic diversity yields increased plant productivity and herbivore performance. *Journal of Ecology* 98: 237–245.
- Laurin-Lemay, S., B. Angers, B. Benrey, and J. Brodeur. 2013. Inconsistent genetic structure among members of a multitrophic system: Did bruchid parasitoids (*Horismenus* spp.) escape the effects of bean domestication? *Bulletin of Entomological Research* 103: 182–192.
- McArt, S. H., and J. Thaler. 2013. Plant genotypic diversity reduces the rate of consumer resource utilization. *Proceedings of the Royal Society of London, B, Biological Sciences* 280: 20130639.
- Mody, K., S. B. Unsicker, and K. E. Linsenmair. 2007. Fitness related diet-mixing by intraspecific host-plant-switching of specialist insect herbivores. *Ecology* 88: 1012–1020.
- Mooney, K. A., and M. S. Singer. 2012. Plant effects on herbivore-enemy interactions in natural systems. In T. Ohgushi, O. J. Schmitz, and R. D. Holt, R. D. [eds.], *Trait-mediated indirect interactions: Ecological and evolutionary perspectives*, 107–130. Cambridge University Press, Cambridge, UK.
- Moreira, X., L. Abdala-Roberts, J. Hernández-Cumplido, M. A. Cuny, G. Glauser, and B. Benrey. 2015a. Specificity of induced defenses, growth, and reproduction in Lima bean (*Phaseolus lunatus*, Fabaceae) in response to multispecies herbivory. *American Journal of Botany* 102: 1300–1308.
- Moreira, X., L. Abdala-Roberts, J. Hernández-Cumplido, S. Rasmann, S. Kenyon, and B. Benrey. 2015b. Plant species variation in bottom-up effects across three trophic levels: A test of traits and mechanisms. *Ecological Entomology* 40: 676–686.
- Moreira, X., L. Abdala-Roberts, S. Rasmann, B. Castagneyrol, and K. A. Mooney. 2016a. Plant diversity effects on insect herbivores and their natural enemies: Current thinking, recent findings, and future directions. *Current Opinion in Insect Science* 14: 1–7.

- Moreira, X., and K. A. Mooney. 2013. Influence of plant genetic diversity on interactions between higher trophic levels. *Biology Letters* 9: 20130133.
- Moreira, X., K. A. Mooney, R. Zas, and L. Sampedro. 2012. Bottom-up effects of host-plant species diversity and top-down effects of ants interactively increase plant performance. *Proceedings of the Royal Society of London, B, Biological Sciences* 279: 4464–4472.
- Moreira, X., W. K. Petry, J. Hernández-Cumplido, S. Morelon, and B. Benrey. 2016b. Plant defence responses to volatile alert signals are population-specific. *Oikos* 125: 950–956.
- Moritz, K. K., C. Björkman, A. L. Parachnowitsch, and J. A. Stenberg. 2016. Female *Salix viminalis* are more severely infected by *Melampsora* spp. but neither sex experiences associational effects. *Ecology and Evolution* 6: 1154–1162.
- Muiruri, E. W., and J. Koricheva. 2016. Going undercover: Increasing canopy cover around a host tree drives associational resistance to an insect pest. *Oikos* doi:10.1111/oik.03307.
- Muiruri, E. W., H. T. Milligan, S. Morath, and J. Koricheva. 2015. Moose browsing alters tree diversity effects on birch growth and insect herbivory. *Functional Ecology* 29: 724–735.
- Naeem, S., J. Thompson, S. Lawler, J. H. Lawton, and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734–737.
- Ninkovic, V., S. A. Abassi, E. Ahmed, R. Glinwood, and J. Pettersson. 2011. Effect of within-species plant genotype mixing on habitat preference of a polyphagous insect predator. *Oecologia* 166: 391–400.
- Ohgushi, T. 2005. Indirect interaction webs: Herbivore-induced effects through trait change. *Annual Review of Ecology, Evolution, and Systematics* 36: 81–105.
- Parker, J. D., J. P. Salminen, and A. A. Agrawal. 2010. Herbivory enhances positive effects of plant genotypic diversity. *Ecology Letters* 13: 553–563.
- Plath, M., S. Dorn, J. Riedel, H. Barrios, and K. Mody. 2012. Associational resistance and associational susceptibility: Specialist herbivores show contrasting responses to tree stand diversification. *Oecologia* 169: 477–487.
- Rodríguez-Saona, C., J. A. Chalmers, S. Raj, and J. S. Thaler. 2005. Induced plant responses to multiple damagers: Differential effects on an herbivore and its parasitoid. *Oecologia* 143: 566–577.
- 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.
- SAS. 2008. SAS, version 9.2. SAS Institute Inc., Cary, North Carolina, USA.
- Scherber, C., N. Eisenhauer, W. W. Weisser, B. Schmid, W. Voigt, M. Fischer, E. D. Schulze, et al. 2010. Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature* 468: 553–556.
- Shimada, T., A. Takahashi, M. Shibata, and T. Yagihashi. 2015. Effects of within-plant variability in seed weight and tannin content on foraging behavior of seed consumers. *Functional Ecology* 29: 1513–1521.
- Siemann, E. 1998. Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology* 79: 2057–2070.
- Staab, M., N. Blüthgen, and A. M. Klein. 2015. Tree diversity alters the structure of a tri-trophic network in a biodiversity experiment. *Oikos* 124: 827–834.
- Tack, A. J., M. T. Johnson, and R. Roslin. 2012. Sizing up community genetics: It's a matter of scale. *Oikos* 121: 481–488.
- Teng, H. J., V. Waddill, F. Slansky, and J. Strayer. 1984. Performance and host preference of adult banded cucumber beetles, *Diabrotica balteata*, when offered several crops. *Journal of Agricultural Entomology* 1: 330–338.
- Thaler, J. S., P. T. Humphrey, and N. K. Whiteman. 2012. Evolution of jasmonate and salicylate signal crosstalk. *Trends in Plant Science* 17: 260–270.
- Tilman, D., P. B. Reich, and J. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441: 629–632.
- Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* 379: 718–720.
- Utsumi, S., Y. Ando, H. Roininen, J. I. Takahashi, and T. Ohgushi. 2013. Herbivore community promotes trait evolution in a leaf beetle via induced plant response. *Ecology Letters* 16: 362–370.
- Van Zandt, P. A., and A. A. Agrawal. 2004. Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). *Ecology* 85: 2616–2629.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology, Evolution, and Systematics* 25: 443–466.
- Zaugg, I., B. Benrey, and S. Bacher. 2013. Bottom-up and top-down effects influence bruchid beetle individual performance but not population densities in the field. *PLoS One* 8: e55317.
- Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer-Verlag, New York, New York, USA.