Received: 13 March 2018 | Accepted: 23 May 2018
DOI: 10.1111/1365-2745.13028

BIOTIC CONTROLS OF PLANT COEXISTENCE

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

A competition–defence trade-off both promotes and weakens coexistence in an annual plant community

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Funding information
H2020 Marie Skłodowska-Curie Actions, Grant/Award Number: 661118-BioFUNC; National Science Foundation, Division of Environmental Biology, Grant/Award Number: 1644641

Handling Editor: Ignasi Bartomeus

Abstract

1. Competition–defence trade-offs have long been thought to promote plant coexistence and increase species diversity. However, insights from modern coexistence theory clarify that such trade-offs alone cannot sustain coexistence. Coexistence also requires stabilising niche differences and the ability of competitor populations to persist under consumer pressure. Despite the breadth of potential consequences of competition–defence trade-offs, we have little mechanistic understanding of how they affect diversity in natural communities.
2. We investigated the effects of seed harvesting by ants on coexistence in an annual plant community. We parameterised a model of plant competitive population dynamics with data from two field experiments: (a) plant demographic rates and competition coefficients determined by growing plants alone and against intra- and interspecific competitor density gradients; (b) plant fitness losses to ant consumers determined by measuring seed removal from experimental depots. We tested for a trade-off between a plant species' demographic potential and its susceptibility to consumption and then determined the bounds of ant effects on pairwise and multispecies coexistence by comparing model projections with and without seed consumption.
3. Ants harvested seeds of all plant species, but they strongly preferred the competitively superior large seeded species, inducing a competition–defence trade-off. Unequal seed loss to ants changed competition-based fitness hierarchies, affecting both the number and identities of plant species pairs that were predicted to coexist compared to a scenario without ants. The trade-off most often prevented coexistence by severely disadvantaging the superior competitor or excluding species directly through overconsumption, and a simulated reduction in the overall consumption rate opened few additional opportunities for coexistence. Ant exacerbation of average fitness differences was particularly disruptive to multispecies coexistence, where niche differences were insufficient to stabilise the coexistence of plant triplets and quadruplets.
4. *Synthesis*. Our results show that the presence of a competition–defence trade-off in a community with stabilising niche differences does not always increase diversity. Instead, the full range of diversity outcomes—positive and negative changes

in species number and changes in the identity of the dominant—are possible. Taken together, our results support the emerging paradigm that consumers have wide-ranging impacts on plant diversity and suggest that variation in consumer pressure may be an important driver of large-scale diversity patterns.

KEYWORDS
annual plant, coexistence, competition, competition–defence trade-off, fitness hierarchy, granivory, harvester ant, seed depot

1 | INTRODUCTION

Plants compete for limited resources and are themselves resources for consumers. Both of these interactions—competition and consumption—reduce plant fitness and are commonly invoked to explain the maintenance of plant species diversity (Chase et al., 2002). In particular, a long-standing argument is that consumers will favour the coexistence of their prey when they preferentially consume the dominant competitors (Paine, 1966). By enforcing this "competition–defence" trade-off among prey species, consumers are expected to weaken the advantage of the superior competitors such that they can no longer competitively exclude the inferior species (Connell, 1961; Holt, Grover, & Tilman, 1994; Paine, 1966).

Advances in coexistence theory have shown that despite the intuitive appeal of this argument, competition–defence trade-offs are insufficient on their own to enable long-term coexistence (Chesson, 2000, 2013; Chesson & Kuang, 2008; Grover & Holt, 1998). Coexistence also requires the stabilising effect of niche differences that were not incorporated in most of the classic papers on competition–defence trade-offs, and which may arise through resource or consumer partitioning (Chesson, 2013; Pacala & Crawley, 1992). In the extreme, even if a competition–defence trade-off was to precisely equalise the fitness of competitors, without stabilising niche differences all but one species will eventually be excluded from a finite community by ecological drift (Adler, HilleRisLambers, & Levine, 2007). Moreover, when these trade-offs do not fully eliminate fitness differences (Chesson, 2000), as would be expected in nature, niche differences set the boundaries that determine how much competitors may differ in average fitness yet still coexist.

In light of modern coexistence theory, we might still predict that consumer preference for the dominant competitor will enable coexistence, but this is true only when three necessary conditions are met. First, there must be niche differences between competitors, mediated by consumers or resources, that are strong enough to stabilise the system (Chesson, 2000, 2013). Second, the dominant competitor's fitness cannot be so strongly reduced by consumers that the inferior competitor gains a fitness advantage that exceeds the stabilising effect of the competitors' niche differences. Third, neither competitor may be so heavily consumed that they cannot achieve positive population growth in the absence of neighbours. If this occurs, the consumer will directly drive one or both competitors to extinction (Holt & Barfield, 2009; Maron & Crone, 2006). These conditions also inform diversity predictions when the consumer preferentially eats the competitive inferior. Here higher consumption of the inferior competitor necessarily increases the average fitness difference between competitors and weakens coexistence.

Although we have outlined the conditions under which a competition–defence trade-off favours or harms the coexistence of a pair of competitors, such trade-offs may also exist in multispecies systems of three or more competitors (Viola et al., 2010). The same logic for coexistence conditions extends to these communities. However, the conditions are complicated by indirect interaction chains that only emerge in these larger systems. For example, intransitive ("rock-paper-scissors") competitive relationships among three or more competitors can allow species that would be excluded in pairwise competition to stably persist in a larger community (Levine, Bascompte, Adler, & Allesina, 2017). Although this complexity challenges the tools of modern coexistence theory developed for pairwise competition, a recently developed "structural" approach allows one to measure multispecies analogues to the pairwise average fitness difference and stabilising niche difference (Saavedra et al., 2017). These tools allow ecologists to measure the effects of consumers on diversity in systems of three or more competitors in ways that account for indirect interactions among competitors.

Because the theoretical expectations for the impact of competition–defence relationships on diversity are so varied, empirical studies are needed to evaluate how consumers affect species diversity via their effects on average fitness differences. Many previous studies have shown that the experimental removal of consumers can reduce diversity within the lower trophic level, implying a competition–defence trade-off that benefits coexistence (Bagchi et al., 2014; Chase, Leibold, Downing, & Shurin, 2000; Edwards, Aquilino, Best, Sellheim, & Stachowicz, 2010; Hillebrand et al., 2007). Nonetheless, other studies have shown the opposite effect wherein the presence of consumers reduces diversity at the lower trophic level (Olffa & Ritchie, 1998; Viola et al., 2010). Despite this large body of empirical work, it is difficult to convincingly demonstrate the underlying trade-offs and relate these trade-offs to coexistence without studies that measure both competitive relationships and consumption effects on average fitness (sensu Chesson, 2000). Indeed, most existing studies that examine either competitor or consumer effects on fitness, or both, do not translate these absolute fitness effects into a measure of a species' ability to exclude others (Larios, Pearson, & Maron, 2017). Of those that do, some are simply observational (e.g., Nottebrock et al., 2017), whereas the experimental studies tend to be restricted to a small number of competitor pairs (e.g., Hanley & Sykes, 2009; Mordecai, 2013). Only with larger numbers of species can empirical studies robustly predict which are most likely to suffer from consumption effects by virtue of their functional traits or shared history with the consumer (Larios et al., 2017; Maron, Hajek, Hahn, & Pearson, 2018).

One of the challenges inherent in empirically determining the effects of consumers on competitive dynamics is the difficulty of translating damage caused by consumers into reductions in the competitors' average fitness. Annual plants consumed by granivores provide an ideal system for overcoming this obstacle because the fitness cost of losing a seed to consumption is clear, and plant competitive relationships can be evaluated in a straightforward manner by combining experiments with mathematical models of community dynamics (Godoy & Levine, 2014). Moreover, granivory is widely distributed in plant communities (Hulme & Benkman, 2009), and granivore exclusion studies, often in annual plant communities, show that these organisms are capable of altering plant community composition (Chen & Valone, 2017; Inouye, Byers, & Brown, 1980; Orrock, Witter, & Reichman, 2008; Peters, Chiariello, Mooney, Levin, & Hartley, 2005).

Here, we examine how consumers influence plant diversity by measuring the effects of granivory by harvester ants on the fitness differences between 42 pairs of annual plant competitors in the context of their competitive niche differences. By pairing field data from plant competition and seed consumption experiments, we tested for a competition–defence trade-off and parameterised an annual plant population dynamics model that predicted the pairwise and 3- and 4-species competitive outcomes in the presence and absence of granivory. Our work thus offers a mechanistic test of how consumers regulate plant diversity at local scales through competition–defence relationships.

2 | MATERIALS AND METHODS

2.1 | Study system

We studied 16 focal plant species (Table 1) from the winter annual community at the University of California Sedgwick Reserve in Santa Barbara County, California, USA (34°41′34″N, 120°02′26″W; 370–730 m above sea level). In the Mediterranean climate of the region, seeds germinate in response to the onset of fall or winter rains (November to December), flower, then disperse seed and senesce in late spring to mid-summer (May to early July). Some seeds do not germinate and remain viable in the soil seedbank.

After dispersal, seeds are vulnerable to a community of vertebrate and invertebrate consumers. Here, we focus on the harvester ant

TABLE 1 Identities of the 16 focal annual plant species along with their native status, mean seed mass, and occurrence in pairwise and structural coexistence analyses. Species were excluded from a coexistence analysis when the competition coefficient matrix had missing data for any species pair. Several species are referred to by updated taxonomic names and identification. Table S1 provides a lookup table for comparing these names to previous work in this plant community

						Frequency in	
Species name	**Species code**	**Family**	**Native**	**Mean seed mass (mg)**	**Pairwise analysis**	**Triplets**	**Quadruplets**
Acmispon wrangelianus	ACWR	Fabaceae	Yes	2.594	Yes	30	49
Amsinckia menziesii	AMME	Boraginaceae	Yes	2.404	Yes	19	26
Centaurea melitensis	CEME	Asteraceae	No	2.800	Yes	32	50
Chaenactis glabriuscula	CHGL	Asteraceae	Yes	0.660	No	0	0
Clarkia bottae	CLBO	Onagraceae	Yes	0.203	No	0	0
Clarkia purpurea	CLPU	Onagraceae	Yes	0.369	Yes	14	16
Erodium botrys	ERBO	Geraniaceae	No	7.159	Yes	15	20
Erodium cicutarium	ERCI	Geraniaceae	No	1.630	Yes	3	1
Euphorbia spathulata	EUSP	Euphorbiaceae	Yes	1.557	Yes	24	36
Festuca microstachys	FEMI	Poaceae	Yes	1.452	No	0	0
Lasthenia californica	LACA	Asteraceae	Yes	0.099	Yes	30	49
Micropus californicus	MICA	Asteraceae	Yes	0.762	No	0	0
Plantago erecta	PLER	Plantaginaceae	Yes	1.717	Yes	32	50
Salvia columbariae	SACO	Lamiaceae	Yes	1.026	Yes	25	40
Silene gallica	SIGA	Caryophyllaceae	No	0.269	No	0	0
Uropappus lindleyi	URLI	Asteraceae	Yes	1.888	Yes	22	31

Veromessor andrei Mayr. This ant species builds large colonies in open areas where our focal plant species occur. Monomorphic worker ants forage in columns that extend up to 10–12 m from the nest (Hobbs, 1985). Although some harvester ant species serve as important seed dispersers by dropping seeds at the nest entrance or out on the landscape, these behaviours are rare in *V. andrei*. Instead, the ants store seeds in nest chambers well below the germination depth of our focal plant species, and viable seeds are rarely found in chaff piles at the nest entrance (Pinter-Wollman, 2015; Wheeler & Creighton, 1934).

2.2 | Annual plant model with seed loss to consumers

We modified a model that describes the dynamics of competing annual plant populations with a seedbank (Levine & HilleRisLambers, 2009) to include seed loss to consumers at a constant, species-specific rate:

$$\frac{N_{i,t+1}}{N_{i,t}} = (1-g_i)(s_i) + \frac{g_i \lambda_i}{1+\alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}}(1-c_i) \qquad (1)$$

where $N_{i,t+1}/N_{i,t}$ is the annual per capita population growth rate of species *i*. $N_{i,t}$ is the number of viable seeds of species *i* that are present in the soil before germination in the fall/winter of year *t*. The first term describes the seedbank dynamics, where $1 - g_i$ is the nongerminating fraction of seeds and s_i is the annual survival probability of seeds in the seedbank. Added to this is a second term that describes the production of new seeds by the fraction of seeds that do germinate, g_i. The per germinant seed production of species *i* in the absence of competition and consumption, λ_i, is reduced through resource competition depending on the density of germinated conspecifics and heterospecifics ($g_i N_{i,t}$ and $g_j N_{j,t}$, respectively) and the per capita competitive effect of germinated species *j* on the per germinant fecundity of species *i* (α_{ij}). The Beverton–Holt functional form for resource competition is well supported by previous work on these plant species (Levine & HilleRisLambers, 2009). We assume that ants consume a fixed proportion, c_i, of the seeds that are produced regardless of the density or identity of surrounding seeds. The fraction of seeds that are not consumed ($1 - c_i$) escape into the soil and—provided that they survive in the soil—are available for germination the following fall/winter.

2.3 | Model parameterisation

In the annual plant life cycle, competition decreases plant fecundity prior to seed dispersal, whereas harvester ants decrease plant fecundity by consuming seeds after dispersal. The separation of these two fitness losses in our field system and in our model means that these processes do not interact within individual plants. That is, individual plants do not have the opportunity to compensate for seed lost to consumers nor do consumers induce defence strategies in attacked seeds (Karban & Baldwin, 2007). Attacked seeds simply die. The noninteractive nature of competitive and consumer effects on plant fitness allowed us to parameterise our model with data from two separate field experiments.

2.3.1 | Experiment 1: Plant intrinsic demographic rates and competition coefficients

For 11 of our focal plant species, we estimated plant demographic parameters (g_i, s_i, and λ_i) and pairwise competition coefficients (α_{ij}) by growing focal individuals of all species across a range of competitor densities. Godoy, Kraft, and Levine (2014) described this design in detail, and the data have been publicly archived (Godoy, Kraft, & Levine, 2017). Briefly, we sowed seeds of each species into replicate plots at densities 0, 2, 4, 8, and 16 g/m^2 of viable seed. Into these competitive backgrounds, we sowed focal seeds of each species. After germination, we measured the density of competitors ($N_{j,t}$) as the number of background plants within a 7 cm radius around each focal plant, and we divided this by the number of background competitor seeds sown into this area to determine the germination fraction (g_j). We estimated seed production of each focal plant, then we used maximum likelihood to estimate seed production in the absence of competitors, λ_i, and the per capita reduction of fitness by competitors, α_{ij}, for all species pairs before seed dispersal (and potential consumption by ants). Seedbank survival (s_i) was estimated by burying seeds in nylon mesh bags and estimating the loss in seed viability at the onset of the next growing season. Because we lack the data to test for fluctuations in these demographic rates and competition coefficients, we assume that they are constant across the spatial and temporal scales of our study.

2.3.2 | Experiment 2: Seed removal rates

We offered seeds of each of 16 annual plant species (Table 1), including the 11 species for which we estimated demographic rates and competition coefficients plus an additional five species to broaden the range of seed masses, native or introduced status, and phylogenetic coverage of our dataset. We subjected seeds of all focal species to foraging harvester ants in the field in 24 replicate "depots" constructed from clear plastic containers (19 × 14 × 10 cm). Each depot had two 3.5 cm diameter holes cut in the centres of adjacent sides that were then covered with 1.5 cm^2 galvanised steel mesh to exclude vertebrate seed consumers. We mixed 20 seeds of each species (10 seeds for the largest seeded species, *Erodium botrys* and *Centaurea melitensis*) and evenly dispersed them on the floor of each depot for a total of 300 seeds per depot. We placed each depot 2 m away from the main entrance of separate *V. andrei* nests and 10 cm away from a foraging trail with a depot entrance hole facing the foraging trail. Replicate ant nests were selected to be at least 20 m apart from one another. We allowed ants to forage from seed depots for 48 hr, beginning at 15:00 on 9 June 2016. Four depots were disturbed by vertebrates, potentially spilling seeds and limiting ant access. These four replicates were excluded from subsequent analyses. The seed depot experiment was located at a different annual plant dominated site on the reserve than the aforementioned competition experiment due to the need for higher ant densities.

We estimated species-specific seed removal rates (c_i) using a generalised linear mixed model (GLMM) with a logit link function. We fit seed species identity as the fixed effect with seed depot as a random intercept using restricted maximum likelihood as implemented in the R package lme4 v.1.1-17 (Bates, Mächler, Bolker, & Walker, 2015).

Motivated by among-species variation in seed removal rates (Figure 1), we tested whether the removal rate was predicted by plant demographic fitness (i.e., a competition–defence trade-off), seed mass, or native vs. introduced status. To test for a competition–defence trade-off, we regressed the proportion of demographic fitness (Equation A.6 in Appendix S1) that was not removed by ants (the proportion of demographic fitness that was "defended") on plant demographic fitness in the absence of consumers. We transformed both variables—using the logit- and log-transformations, respectively—to linearise each prior to fitting the regression. To test whether plant attributes predicted seed removal rates by ants, we calculated the mean seed mass of each species by weighing 30 individual seeds to the nearest 0.001 mg, and we determined plant native status following the Jepson manual (Table 1; Baldwin et al., 2012). We constructed a phylogenetic tree to control for potential phylogenetic nonindependence of the seed removal rate in these tests. We grafted our focal species (Table 1) onto an angiosperm tree topology (Phylocom v.4.2; Webb, Ackerly, & Kembel, 2008) with branch lengths that are consistent with prior knowledge of the divergence times of major angiosperm clades (Wikström, Savolainen, & Chase, 2001). We tested for phylogenetic signal in seed removal rate using Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg, Garland, & Ives, 2003) as implemented in the R package ape v.5.1 (Paradis, Claude, & Strimmer, 2004). We regressed seed removal rate on seed mass with nativity as a covariate using phylogenetic least squares assuming Brownian evolution of the seed removal rate as implemented in the packages ape v.5.1 (Paradis et al., 2004) and nlme v.3.1-137 (Pinheiro, Bates, DebRoy, & Sarkar, 2017). As seed removal rates were highly labile among our relatively small number of species, we fit alternative models with Pagel's $\lambda = 0$ and $\lambda = 1$ to understand how our results could be affected by phylogenetic nonindependence. The results were qualitatively similar to the model fit using the empirically estimated phylogenetic signal (Table S2), and we do not discuss them further.

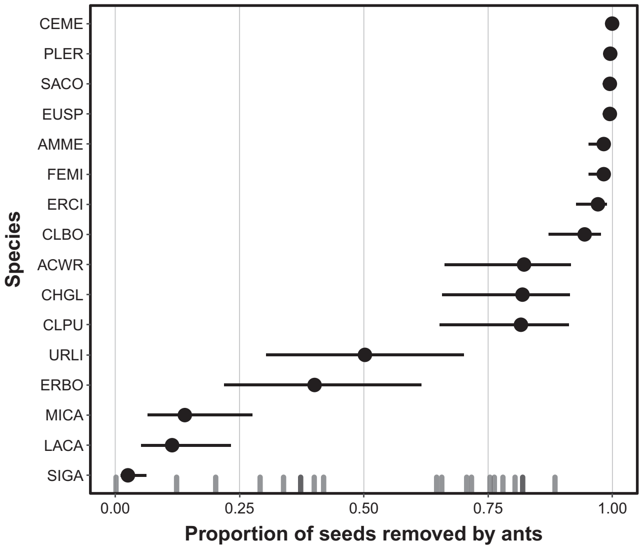

FIGURE 1 Proportion of seeds that *Veromessor andrei* removed from experimental depots. Removal rates are shown by plant species (fixed effect; black points; mean ± 1 SEM) and depot (i.e., nest; random effect; grey ticks along *x*-axis) estimated from a generalised linear mixed model with binomial errors and a logit-link. Four-letter species codes correspond to full species names in Table 1

2.4 | Ant effects on plant coexistence

2.4.1 | Pairwise analyses

To evaluate how ants affect the coexistence of species pairs, we made a number of key assumptions. First, we assumed that all seeds removed from the depots were either consumed by ants or were otherwise removed from the population. This simplification is consistent with the observations that *V. andrei* seldom drop seeds while returning to the nest (W. K. Petry, pers. obs.; Brown & Human, 1997), the ants nest deeper than the annual plant seedbank (Pinter-Wollman, 2015) and rarely reject intact seeds of our focal species at the nest entrance (W. K. Petry, pers. obs.; Wheeler & Creighton, 1934; Pinter-Wollman, 2015). Second, we used consumption rate estimates from the full dataset, despite not having demographic and competition data for five species (Table 1). Excluding these had no qualitative effect on preference rank and had little quantitative effect on the consumption rates estimated (consumption rates from model with all 16-species vs. 11-species subset $r = 0.9999$). Third, we assumed that the consumption rates and preferences we measured in our seed depot experiment reflected the consumption rates over the entire foraging season. A previous study of *V. andrei* foraging preferences over the season suggested that preferences are relatively stable over time when the same composition of seeds was offered in 24 hr trials (Hobbs, 1985). Similarly, harvester ant seed preferences have been reported to be consistent from short-term seed depot trials (60 min and 5 days) to seedling recruitment responses in the subsequent growing season (Pearson, Icasatti, Hierro, & Bird, 2014). Lending further support to our assumption, *V. andrei* has an especially short foraging season (*c*. 2 months, late April to late June) coinciding with seed dispersal (W. K. Petry, pers. obs.). Within this period, foragers are active in the few hours around sunrise and sunset (Creighton, 1953; Hobbs, 1985; W. K. Petry, pers. obs.).

Following prior work with the annual plant competition model in the absence of seed consumption (Chesson, 2013; Godoy & Levine, 2014; Godoy et al., 2014; Kraft, Godoy, & Levine, 2015), we can update the niche and fitness difference terms to include (c_i). From Equation 1, it can be seen that ($1 - c_i$), the unconsumed fraction of seeds, simply scales λ_i. Thus, wherever λ_i appears in the expression for niche or fitness differences from Godoy and Levine (2014), it needs to be scaled by (1 − c_i).

The stabilising niche difference (1 − ρ) was shown by Godoy and Levine (2014) to be:

$$(1-\rho)=1-\sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{jj}\alpha_{ii}}} \qquad (2)$$

This term captures the degree to which competition is stronger within vs. between species and thus characterises how well each species is able to recover when depressed to low density. The niche difference is independent of the intrinsic fecundity, λ_i, and thus, it is also unaffected by constant species-specific rates of seed consumption (c_i).

In contrast, the average fitness difference in Godoy and Levine (2014) contains the intrinsic fecundity term, and thus is scaled to include seed consumption accordingly:

$$\frac{\kappa_j}{\kappa_i}=\left(\frac{\frac{g_j\lambda_j(1-c_j)}{1-(1-g_j)(s_j)}-1}{\frac{g_i\lambda_i(1-c_i)}{1-(1-g_i)(s_i)}-1}\right)\sqrt{\frac{\alpha_{ij}\alpha_{ii}}{\alpha_{jj}\alpha_{ji}}} \qquad (3)$$

The average fitness difference determines the rate at which the superior competitor excludes the inferior. It is composed of the ratio of the two species' demographic fitness (seeds produced per seed lost from the seedbank) scaled by seed consumption as well as the species' relative response to competition quantified in the square root term. High demographic fitness and low sensitivity to competition (i.e., low α_{ii} and α_{ij}) produce stronger competitors.

Chesson (2000) showed that the condition for a fitness inferior competitor species *i* to coexist with a fitness superior competitor species *j* is:

$$\rho<\frac{\kappa_i}{\kappa_j} \qquad (4)$$

We evaluated this condition for each species pair without seed consumption ($c_i = 0$) and again with our empirically estimated seed consumption rates (c_i from Figure 1) to determine the range of ant effects on pairwise coexistence.

2.4.2 | Sensitivity of pairwise coexistence to the seed consumption rate

We chose to place seed depots near ant nests and foraging trails to estimate the upper bound of ant effects on plant fitness differences. However, the estimated consumption rates are likely to be inflated relative to the consumption rate farther from the nest. To explore the consequences of lower overall consumption rates, we systematically simulated a reduction of seed consumption rates of all plant species by a constant proportion and then reassessed the ability of each plant species pair to coexist. Importantly, this approach does not affect the preference ranking of species and thus decouples the effect of the overall consumption rate from effect of the competition–defence relationship. We approximated the continuous variation of the scaling factor by determining all pairwise diversity outcomes at 10,000 points spaced evenly between zero (identical to the "no ant" scenario) and one (identical to the empirically estimated seed consumption rate).

2.4.3 | *n*-species analyses

Indirect interactions may enable coexistence of multispecies communities even when pairwise metrics predict competitive exclusion; for example, a three-species rock–paper–scissors intransitive loop in competitive ability may allow all three species to coexist but prevent the coexistence of any constituent species pair (Billick & Case, 1994; Levine et al., 2017). Previous work on this annual plant community suggests that such interaction chains and higher order interactions have little effect on diversity in our system (Godoy, Stouffer, Kraft, & Levine, 2017). Does seed consumption by ants—through its effects on the strength and direction of pairwise fitness advantages—enable more multispecies communities to coexist or destabilise multispecies communities that coexist through higher order interactions?

To address this question, we used the structural approach to coexistence (Saavedra et al., 2017) to quantify the analogues of average fitness and niche differences for all three- and four-species combinations, excluding those combinations without all the required pairwise competition coefficients and those for which there was no locally stable equilibrium. We used the *D*-stability of the competition coefficient matrix as the criterion for local stability of equilibrium population sizes (Johnson, 1974; Logofet, 2005) based on 10^4 and 10^5 simulations for each set of triplets and quadruplets, respectively. There is no criterion for assessing the global stability of these equilibria with the annual plant competition model (Equation 1; Case, 2000; Saavedra et al., 2017). To determine the coexistence of species within triplets and quadruplets, we used each community's pairwise competition coefficients (α_{ij}) to calculate the feasibility domain of the community (D_F), that is, the set of intrinsic growth rates that allow each component species to have a positive abundance at equilibrium (analogous to the shaded coexistence region in Figure 4). We also determined the centroid of the feasibility domain, $\mathbf{r}_c$, which is the vector of the intrinsic growth rates that would result in equal average fitness among all species in the community (analogous to the κ_j/κ_i = 1 horizontal line in Figure 4). We then determined the vector of observed intrinsic growth rates with ($\mathbf{r}^+$) and without ($\mathbf{r}^-$) seed consumption by ants. The angle between these two vectors and the centroid of the feasibility domain, $\mathbf{r}_c$, corresponds to the structural analogue of fitness differences when ants are present (θ^+) versus absent (θ^-).

Because ants do not influence niche differences in our model (i.e., seed consumption rates are assumed to be fixed within species), the feasibility domain (D_F) is unaffected by ants and the structural analogue of the niche difference (the normalised solid angle of the feasibility domain; Ω) is identical under both ant scenarios. As such, our model does not allow ants to affect plant diversity by altering the strength of pairwise interactions nor the structure of indirect interactions in *n*-species communities ("community-pair overlap" and "community-pair differential," respectively, sensu Saavedra et al., 2017).

3 | RESULTS

Ants removed 70.7% of seeds across all included depots. Although the mean removal rate was high, the rates differed significantly between species (Figure 1; Table S3; $\chi^2_{(15)} = 3488.3$, $p < 0.001$), with eight species seeing nearly all their seeds removed while one had nearly no seeds removed. Removal rates were also heterogeneous among depots (i.e., nests), with the adjacent ant colonies collecting 0.2%–88.4% of available seeds (Figure 1; $\sigma_{\mathrm{depot}} = 0.87$).

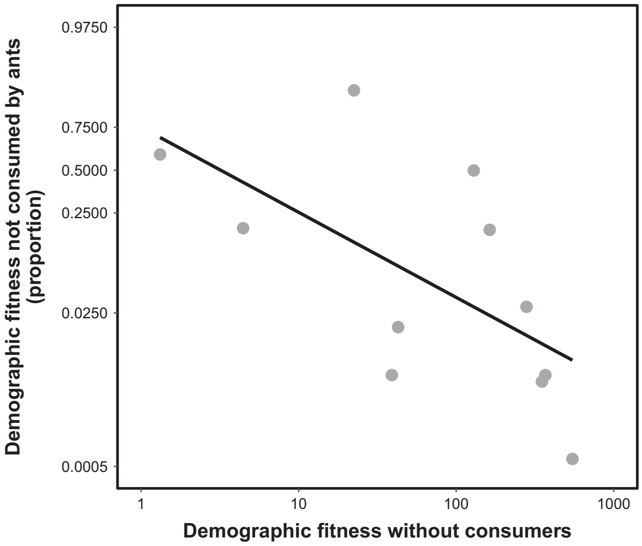

FIGURE 2 Among-species trade-off between intrinsic seed production and the proportion of seeds that escape ant consumption. Plant species with higher seed production in the absence of competitors and consumers (η_i; Equation A.6 in Appendix A) are more heavily consumed by ants. Each point represents one plant species. Note that seed consumption rates are plotted on a logit scale whereas growth rates are plotted on a logarithmic scale. This relationship does not appear to be strongly controlled by any single component of demographic fitness (Figure S1)

We found evidence for a strong competition–defence trade-off (Figure 2). Plant demographic fitness varied by 2.6 orders of magnitude among our focal species, wherein the seeds of the species with the highest demographic fitness were 92 times more likely to be removed from depots by ants than were the seeds of species with the lowest demographic fitness. Among the 42 species pairs for which we had competition data, the competition–defence trade-off reversed the demographic fitness advantage in more than half of them (23 pairs). Seed removal rates showed very little phylogenetic signal (Figure 3a; Pagel's $\lambda < 0.001$, $p = 1$; Blomberg's K = 0.404, $p_{\mathrm{PERM}} = 0.338$) among our focal species, a subset of the annual plant community at our field site. Ants collected large seeds at higher rates across the range of seed masses encompassed by our focal species (Figure 3b; $F = 4.85$, $df = 1, 12$, $p_{\mathrm{PGLS}} = 0.048$; range 0.1–2.8 mg, excluding the outlier ERBO). Seed removal rates did not differ between native and introduced species when controlling for seed mass and phylogeny (Figure 3c; $F = 0.45$, $df = 1, 12$, $p_{\mathrm{PGLS}} = 0.517$).

We found that ants had strong effects on the outcome of pairwise plant competition when the mean seed removal rate for each species was taken as the seed consumption rate. In the absence of seed consumption by ants ($c_i = 0$ for all species), we found that two of 42 plant species pairs had sufficient niche differences to stabilise their average fitness differences and allow for coexistence. When we instead incorporated the empirical estimates of seed consumption by ants (Figure 1), the consumptive effects of ants on average fitness differences had profound qualitative effects on plant diversity (Figure 4). Neither of the two species pairs coexisting in the absence of ants (ACWR-CEME and SACO-CEME) could coexist after ants magnified their average fitness differences. However, in one other species pair (SACO-PLER), ants preferentially consumed the superior competitor enough to equalise fitness differences and allow for stable coexistence. The far more common outcome was that ants

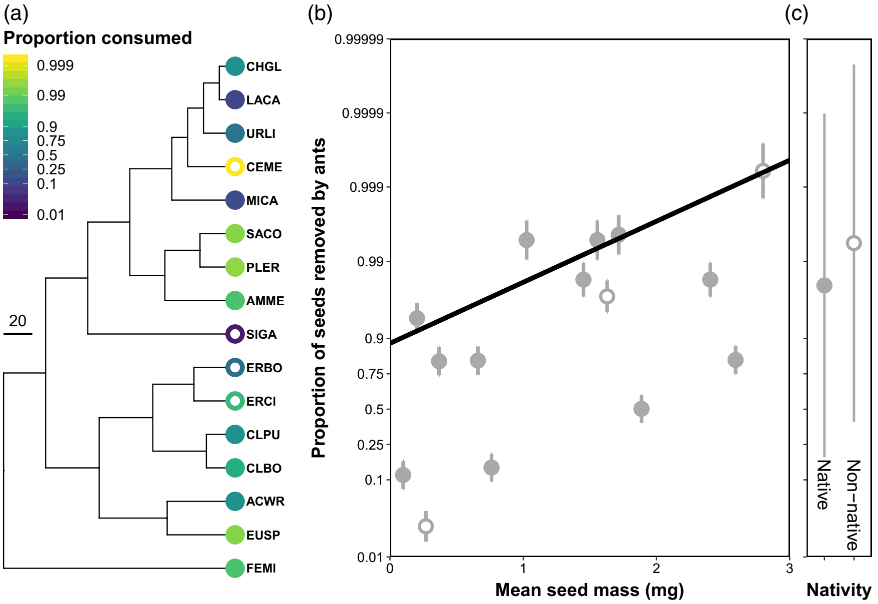

FIGURE 3 Seed removal rates by phylogenetic relatedness, nativity, and seed mass. (a) Phylogenetic relationship of the focal plant species with seed removal rates mapped onto the branch tips. The scale bar units are millions of years. (b) Relationship between seed mass and seed removal rate for the focal plant species. The solid line shows the statistically significant linear fit (see main text for statistics). ERBO has been excluded as an outlier (mass >7 × the interquartile range). (c) Plant nativity has no marginal effect on seed removal rate by ants after controlling for seed mass (see main text for statistics) [Colour figure can be viewed at wileyonlinelibrary.com]

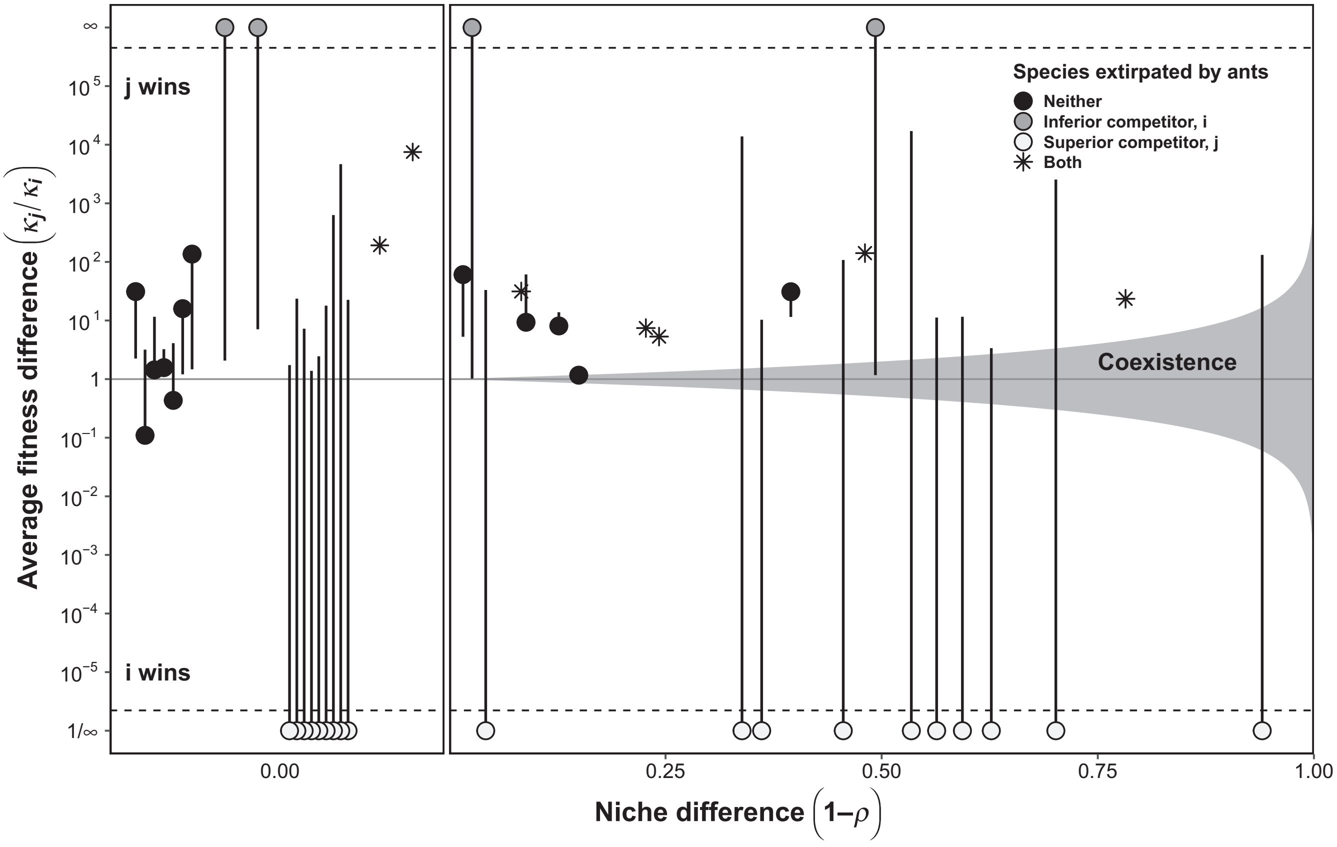

FIGURE 4 Effects of ant seed consumption on pairwise average fitness differences and coexistence in an annual plant community. Each point represents a species pair with respect to their average fitness (κ_j/κ_i; *y*-axis) and niche ($1 - \rho$; *x*-axis) differences when granivorous ants are present. The width of the *x*-axis around 0 is enlarged to show the 20 species pairs with perfect niche overlap ($1 - \rho = 0$). Each point has a tail showing where the species pair occurs in this space when ants are absent. All tails begin where $\kappa_j/\kappa_i > 0$ because we arbitrarily assigned the superior resource competitor as species *j*. Moreover, all tails are vertical because our design did not allow consumers to affect species niche differences (see Section). The background colour indicates the regions of stable coexistence (grey), of competitive exclusion (upper white: species *j* > *i*, lower white: species *i* > *j*). Points are filled according to the ability of seed consumption by ants to drive the plant species to extinction directly, even in the absence of competitors. Both species may have positive competitor-free growth despite seed consumption (black) or may be extirpated by ants (asterisk). The intermediate scenarios where only one plant species is extirpated by ants are shown in grey (dark = the inferior resource competitor species *i*, light = the superior resource competitor species *j*)

ate such a large fraction of the seeds that one (23 species pairs) or both (7 species pairs) of the competitors were predicted to be locally extirpated by ants.

Reducing the overall seed consumption rate while maintaining the species preference hierarchy had little effect on the number of species pairs that were able to coexist (Figure 5). Instead, ants were less able to directly exclude plant species via seed overconsumption as the overall consumption rate was scaled down, and the qualitative outcomes rapidly approached the ant-free projections. Even for the species pairs in which ants reversed the identity of the excluded species (Figure 4, light grey points), the average fitness differences tended to be highly sensitive to the scaling factor near average fitness equality, the region where niche differences—if present—could stabilise coexistence (Figure S2).

Only 16 species triplets and four species quadruplets had locally stable equilibria as determined by the matrix of their pairwise competition coefficients (α_{ij}). None of these multispecies communities were able to coexist in the absence of ants nor did seed consumption enable coexistence by reducing the structural analogue of average fitness differences (θ). Instead, ants increased this average fitness difference in triplets by an mean of 40.9° (paired $t_{15} = 4.49$, $p < 0.001$) and in quadruplets by 34.6° (paired $t_3 = 2.59$, $p = 0.081$). Thus, on average, ants diminished the opportunities of three- and four-species communities to coexist, but simultaneously allowed different pairwise subsets of these communities to coexist (Figure S3, Table S4).

4 | DISCUSSION

Plant diversity has long been recognised to be governed by both competition and consumption, with competition–defence trade-offs functioning as important diversity-maintaining mechanisms. We tested this claim using models parameterised with field experiments and interpreted in light of modern coexistence theory to predict whether the coexistence of annual plant species pairs, triplets, and quadruplets was affected by preferential seed consumption by

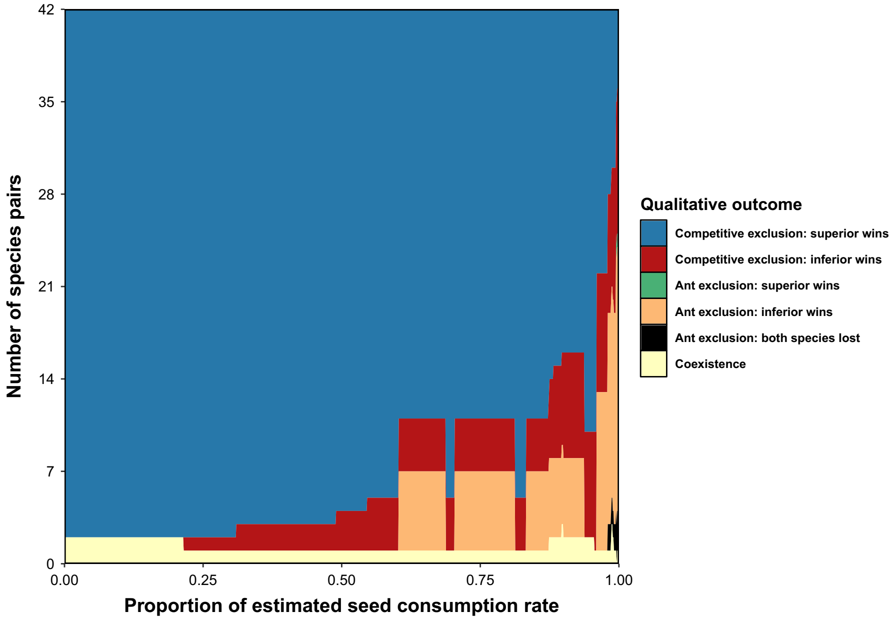

FIGURE 5 Sensitivity of pairwise plant competitive outcomes to seed consumption rates. Scaling the empirically estimated seed consumption rate (*x*-axis) affects the number of species pairs (*y*-axis) that fall under each qualitative interaction outcome (fill colour). The number of coexisting species pairs (light yellow) is insensitive to the overall seed consumption rate. Over most of the parameter space, the superior competitor excludes the inferior competitor (blue). Moderate consumption rates sometimes advantaged the inferior competitor by allowing it to competitively exclude the superior competitor (red) or freed it from competition when ants directly extirpated the superior competitor (pale orange). Only at extreme consumption rates did ant overconsumption extirpate the inferior competitor (pale green; very few cases) or both species (black) [Colour figure can be viewed at wileyonlinelibrary.com]

harvester ants. Although we found a competition–defence trade-off among plant species where harvester ants preferentially consumed the larger seeded competitors with higher demographic fitness (Figures 2 and 3), the effect of ants on the maintenance of plant species diversity was mixed (Figure 4). Ants reshuffled the demographic fitness advantages among plant species pairs, exacerbating the average fitness differences between some, diminishing the average fitness differences of others, and reversing still others. Rather than enabling coexistence by equalising fitness among competitors, seed consumption more often resulted in the superior competitors being excluded from the community directly by ant overconsumption. This tended to allow the inferior competitor to persist in pairwise analyses, but it also weakened coexistence in multispecies communities by increasing the structural analogue of average fitness differences.

Although *V. andrei* ants are generalist seed consumers, they exhibited strong species preferences (Figure 1) that could be partially explained by species seed mass (Figure 3). Ants preferred larger seeds, but even the 28-fold variation in seed mass of our focal species (0.1–2.8 mg, excluding the outlier ERBO) was insufficient to reveal an optimum seed size beyond which we expect seed removal rates to decline. Seed size selectivity is common in harvester ants, with preferences corresponding to the relative sizes of foragers and the seeds they encounter (e.g., Hobbs, 1985; Kaspari, 1996; Kelrick, MacMahon, Parmenter, & Sisson, 1986; Pirk & de Casenave, 2010). The preferences of *V. andrei* for large seeds corresponds to the predictions of adaptive foraging theory given the presumed (a) higher food value of large seeds, (b) low-handling costs due the proximity of depots to ant nests in our experiment (2 m; Detrain & Deneubourg, 2009), and (c) proportionally higher cracking forces required to access nutritive tissue in small seeds (Fricke & Wright, 2016). The power of this single trait to predict seed removal by ants—and thus, the demographic component of average fitness differences—parallels the correlations between individual plant functional trait and plant demographic ratios in the absence of seed consumption in this community (Kraft et al., 2015). In contrast to ant size selectivity, we did not find evidence for enemy release of nonnative plant species (reviewed by Liu & Stiling, 2006; Pearson et al., 2014). Nonnative species had no significant difference in seed mass or ant consumption rate (Figure 3), albeit the sample sizes for these tests were relatively small. Moreover, nonnative species in this community tend to have other demographic advantages over native species that may better explain their invasion and persistence (Godoy & Levine, 2014).

Ant seed preferences had community-level consequences for plant species diversity, driven largely by ant preferences for the larger seeded superior competitors (Figures 3 and 4). Among the pairs of plant competitors, ants most frequently reversed the competitive asymmetry between species, overshooting the region of coexistence such that the inferior competitor replaced the superior competitor as the lone persisting species. Still, a minority of cases exhibited a broader range of ant effects, including exacerbating the superior competitor's fitness advantage (nine species pairs), enabling coexistence by equalising average fitness differences to within the range that was stabilised by niche differences (one pair: SACO-PLER) and reducing diversity to zero by driving both species to local extinction (seven species pairs composed of five plant species). This wide range of ant effects on plant diversity arose despite the competition–defence trade-off in our community (Figure 2), in part because some competitors had insufficient niche differentiation to stabilise coexistence (e.g., Figure 4, left panel) but more often because consumption drove the superior competitors to extinction. Our results provide a mechanistic complement to previous vegetation surveys in both a similar annual plant community where *V. andrei* was found to both increase and decrease the abundances of individual plant species around ant nests (Peters et al., 2005; Samson, Philippi, & Davidson, 1992; but see Brown & Human, 1997) and in other plant-harvester ant communities (e.g., Guo & Brown, 1996; Inouye et al., 1980).

Our finding that ants have diverse effects on plant competitive outcomes provides strong empirical evidence against the classic paradigm that consumers and competition-consumption trade-offs generally increase diversity. Although we found high rates of seed removal, they were consistent with consumption rates near nests in other communities (e.g., Hobbs, 1985). In our sensitivity analysis, reducing the overall consumption rate while maintaining the trade-off with demographic competitive ability failed to provide many new opportunities for coexistence (Figure 5, Figure S2). This suggests that our inability to find widespread coexistence as a result of the competition–defence trade-off was not an artefact of extreme consumption rates. At lower rates of overall consumption, the identities of the excluded species varied (Figure S2), suggesting that variation in ant foraging pressure may allow for additional consumer-mediated coexistence mechanisms across the landscape or at longer time-scales (Chesson, 2013). Still, we observed nearly the full range of variation-independent consumer effects on diversity predicted by theory (Chesson, 2013; Chesson & Kuang, 2008) in our small plant community with a single consumer species. As such, our results contribute to the growing body of empirical literature showing that the interplay of competition and consumption shapes species diversity of plant communities (Maron et al., 2018; Mordecai, 2013; Nottebrock et al., 2017; Parker & Gilbert, 2018).

Pairwise analyses of the mechanisms that maintain diversity can be misleading when they obscure coexistence that arises through interaction chains that are only possible in more diverse systems (Billick & Case, 1994). By applying a structural extension of modern coexistence theory (Saavedra et al., 2017) to our empirical data, we found that ants never favoured the coexistence of species triplets and quadruplets. Instead, ants tended to push the vector of plant intrinsic population growth rates farther away from the sets of growth rates that would allow for coexistence of more than two species ($\theta^+ > \theta^-$; Figure S3). Importantly, we were forced to exclude the majority of potential species triplets and quadruplets from analysis because we lacked one or more of the necessary pairwise competition coefficients or the resulting communities failed to have a locally stable equilibrium point (Table S4). Still, previous work on a larger number of species from our study community suggests that these indirect effects on plant diversity are also relatively uncommon via competition alone (Godoy, Stouffer, et al., 2017; Saavedra et al., 2017).

Our study documents the mechanistic link between ant granivory and local plant diversity through ant effects on plant demographic fitness. However, our results come with several important limitations. First, our model assumes that ants consume seeds at a spatially and temporally constant and density-independent rate for each plant species, estimated as the mean removal rates from our seed depots (Figure 1). This simplification makes the calculation of niche and average fitness differences analytically and empirically tractable. However, in so doing, we exclude the stabilising effects of consumer-mediated niche differentiation that could arise when seed consumption rates are density- or frequency-dependent. Observational evidence suggests that harvester ant seed preferences are relatively constant across the foraging season (Hobbs, 1985; Pearson et al., 2014), but to our knowledge, this apparent stability has not been experimentally tested in *V. andrei* nor must preference stability be true for other granivores like rodents and birds. Similarly, apparent competition through a shared consumer may counter the stabilising effect of resource-based niche partitioning because the stabilising effects of resource and consumer niches are generally nonadditive (Chesson, 2013).

A second caveat is that consumer pressure is likely to be highly variable over space and time at our field site. As part of a separate study, we mapped all ant nests in our 9.4 ha study site in 2017, and we found that *c*. 50%–80% of the area was within the 10–15 m foraging range of *V. andrei* (Hobbs (1985); W. K. Petry, unpubl. data). About 5%–7% of our study area is within 2 m of an ant nest and thus subject to the upper bound of seed removal rates that our study was designed to capture (Figure 1). Foraging intensity necessarily decreases with distance from the nest as foragers must search increasingly large areas at the limits of the foraging range and likely return to distant locations with lower frequency. Moreover, it is possible that the discovery rate or relative value of seeds changes with distance, and these may interact with seed species identity to affect harvesting rates (Crist & MacMahon, 1992). Finally, the locations and sizes of ant colonies are not fixed. New colonies establish whereas existing colonies change size, die, and occasionally relocate their nest, albeit over short distances (Pinter-Wollman & Brown, 2015). Taken together, the natural history of harvester ants in our study system suggests that spatiotemporal variations in seed consumption may play an important role in the maintenance of plant diversity across the landscape over and above the local mechanisms we explore here.

In conclusion, we have demonstrated that competition–defence trade-offs can be potent regulators of diversity, but that such trade-offs do not necessarily promote long-term coexistence. Instead, our relatively small plant community with a single consumer species and a simplified model of consumer effects on producers—limited to variation-independent changes in average fitness differences—yielded a wide range of the diversity outcomes that are consistent with the predictions of modern coexistence theory. More generally, our results provide an explanation for why diversity is not always higher in communities where competition–defence trade-offs arise. Predicting diversity in these communities will necessarily require not only the measurement of species responses to competitors and consumers but also the translation of these responses to population dynamics and contextualisation with species' niche differences that are essential for stabilising long-term coexistence.

ACKNOWLEDGEMENTS

We are grateful to Mirjam von Rütte for her assistance in the field, to John Orrock for advice on seed depot design, to Kate McCurdy and the staff of the UCNRS Sedgwick Reserve (https://doi.org/10.21973/n3c08r) for field site support, and to Kailen Mooney for laboratory space and equipment to process field samples. Andy Kleinhesselink provided updated plant species identifications and taxonomy, and Will Pearse provided advice on phylogenetic methods. Two anonymous reviewers provided constructive commentary that greatly improved the manuscript. NJBK, JML, and GSK were supported by the National Science Foundation DEB-1644641. OG acknowledges postdoctoral financial support provided by the European Union Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement no. 661118-BioFUNC.

AUTHORS' CONTRIBUTIONS

W.K.P. and J.M.L. developed the study idea; O.G., N.J.B.K., and J.M.L. designed the competition experiment and collected the plant demographic data; N.J.B.K. analysed the competition data to estimate plant demographic rates and competition coefficients; W.K.P. designed the seed removal experiment and collected the data with N.J.B.K. and G.S.K.; O.G. built the phylogeny; W.K.P. analysed the data and drafted the manuscript. All authors provided critical feedback on manuscript drafts, responses to reviewers, and approved the final version.

DATA ACCESSIBILITY

Plant demographic and resource competition data have previously been archived (Godoy et al., 2014; Godoy, Kraft, et al., 2017). Raw data for ant seed removal from seed depots, seed mass data, and all code needed to reproduce the analyses are available at https://doi.org/10.5281/zenodo.1256658 (Petry, Kandlikar, Kraft, Godoy, & Levine, 2018).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Petry WK, Kandlikar GS, Kraft NJB, Godoy O, Levine JM. A competition–defence trade-off both promotes and weakens coexistence in an annual plant community. *J Ecol*. 2018;106:1806–1818. https://doi.org/10.1111/1365-2745.13028