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Competition as a mechanism structuring mutualisms

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Summary

1. Hutchinsonian niche theory posits that organisms have fundamental abiotic resource requirements from which they are limited by competition. Organisms also have fundamental biotic requirements, such as mutualists, for which they also might compete.

2. We test this idea with a widespread ant–plant mutualism. Ant-mediated seed dispersal (myrmecochory) in eastern North America involves a few ant species that can effectively disperse the seeds of many plant species. This imbalance suggests that ant-dispersed plants (myrmecochores) might compete for ant dispersers. We hypothesized that, because larger seeds are more attractive to ants, myrmecochores might segregate the timing of seed release by size to relieve competition.

3. Comparative literature analysis across plant species reveals that myrmecochore seed size increases with the fruiting season in a staggered pattern so that small- and large-seeded co-occurring species do not release seeds at the same time – a pattern not observed in plants using other dispersal modes.

4. We then presented foraging ants with small and large seeds in field trials throughout the fruiting season to test whether the observed temporal segregation in myrmecochore seed size is consistent with plant competition for ant dispersers.

5. Our results show that dispersal rates for smaller seeds increase across the growing season, but only in the absence of large seeds. Our combined literature and field data suggest that myrmecochores stagger fruiting by seed size so that small seeds are set earlier to avoid competition for dispersal mutualists with larger seeds.

6. *Synthesis*. Ecological interactions are often treated as either positive or negative, but our data blur this distinction by revealing that a positive interaction (mutualism) might be structured by a negative interaction (competition). Moreover, the recognition of biotic resources as critical niche requirements blurs the classic dichotomy between the fundamental (abiotic) versus realized (biotic limited) niche.

Key-words: ant–plant interactions, *Aphaenogaster*, biotic interactions, dispersal, niche theory, seed dispersal, species distribution

Introduction

Long-standing ecological theory connects population success with optimal niche requirements (e.g. light, temperature and nutrients), where resource access is limited by negative interactions among species (Hutchinson 1957). However, recent work suggests that, whereas competition might limit access to resources, positive biotic interactions might augment access (Bronstein, Wilson & Morris 2003; Bruno, Stachowicz & Bertness 2003; Bronstein 2009). Yet a mutualist partner also can be viewed as a resource, such as when animal-mediated pollination or seed dispersal are required for population persistence (Jones, Bronstein & Ferriere 2012). Plant–disperser mutualisms should then co-evolve with selection favouring plant-based mechanisms that attract mutualist partners to their seeds (Hanzawa, Beattie & Culver 1988; Cain, Damman & Muir 1998; Vander Wall 2001; Burns 2002; Herrera 2002; Palmer, Stanton & Young 2003). If mutualists indeed compete for partners, it blurs the classic niche dichotomy between a fundamental niche defined by abiotic requirements and a contracted realized niche where access to resources is mediated by biotic interactions. Instead, biotic resources (e.g. dispersal mutualists) may be considered fundamental niche requirements.

For example, successful pollination is a niche requirement for population persistence. Competition for the ‘pollinator resource’ among plant species likely led to the evolution of

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*Correspondence author. E-mail: hexastylis@gmail.com segregated pollination timing (Palmer, Stanton & Young 2003; Pauw 2013). This segregation then staggers pollination demands across the season, which presumably minimizes simultaneous demand for mutualist partners (Schemske *et al.* 1978; Pauw 2013). Similar ideas about the structuring role of competition on seed timing are less developed for dispersal mutualisms. It has been suggested, but not tested, that plants may stagger seed set to reduce competition for animal foragers that disperse their seeds (Beattie & Culver 1981; Handel, Fisch & Schatz 1981; Heithaus 1986; Smith *et al.* 1989; Ruhren & Dudash 1996).

Whereas long-distance dispersal helps plants colonize new habitats, localized dispersal (including animal-mediated) is required to maintain existing populations, making dispersal a fundamental component of population persistence (Pulliam 1996; Nathan & Muller-Landau 2000; Hanski 2001; Bullock *et al.* 2002; Bruno, Stachowicz & Bertness 2003). As such, observational evidence suggests that plants may compete for dispersers (Howe & Estabrook 1977; Davidson & Morton 1981; Herrera 1981; Wheelwright 1985). If dispersers are a fundamental niche requirement, then plant species coexistence may depend on species partitioning (MacArthur & Levins 1967) their disperser resource. In this study, we combine literature analysis with field experimentation to test the hypothesis that a guild of ant-dispersed plants in eastern U.S. deciduous forests compete for dispersal by their ant partners resulting is size-segregated seed release.

More than 10 000 plant species world-wide possess specialized adaptations to induce seed dispersal by ants (Mayer, Olzant & Fischer 2005; Rico-Gray & Oliveira 2007; Ness, Morin & Giladi 2009; Lengyel *et al.* 2010). Ant-dispersed plants (myrmecochores) attract ants via a lipid-rich appendage on the seed known as an elaiosome (Marshall, Beattie & Bollenbacher 1979; Skidmore & Heithaus 1988; Pizo & Oliveira 2001). Ant-mediated seed dispersal reduces plant clumping (and its negative consequences), reduces seed predation, allows colonization of novel habitat and provides seedlings with nutrient-rich environments for establishment (see Gorb & Gorb 2003; Giladi 2006; Rico-Gray & Oliveira 2007 and references therein). Ants therefore provide a service (dispersal) for a reward (elaiosome; *sensu* Jones, Bronstein & Ferriere 2012).

Myrmecochory is asymmetrical in two important ways. First, the mutualism appears obligate for plants and facultative for ants (Ness, Morin & Giladi 2009; Clark & King 2012). Secondly, effective seed-dispersing ant species are not as speciose as the plants that use them (Gove, Majer & Dunn 2007; Rey & Manzaneda 2007; Ness, Morin & Giladi 2009). For example, eastern North American (N.A.) woodlands host >50 plant species with seeds adapted for ant dispersal (Beattie & Culver 1981; Handel, Fisch & Schatz 1981; Cain, Damman & Muir 1998; Mitchell, Turner & Pearson 2002), but only 2–4 ant species effectively disperse these seeds (Ness, Morin & Giladi 2009; Warren, Giladi & Bradford 2010). The diversity of partners (i.e. effective seed-dispersing ants) in N.A. woodlands is particularly low – lower than in myrmecochory in other ecosystems and lower than some other forms of animal–plant mutualisms, such as frugivory (Ness, Morin & Giladi 2009). Plant dependence on ant dispersers corresponds with seed phenology, morphology and chemistry adaptations that maximize seed interest by the most effective seed-dispersing ants (Turnbull & Culver 1983; Hughes & Westoby 1992; Espadaler & Gomez 1996; Boulay *et al.* 2007; Rico-Gray & Oliveira 2007). A mutualism with specific dispersers necessitates that plants release seeds when those dispersers are available and are most attracted to seeds (Harper 1977; Thompson 1981; Oberrath & Boehning-Gease 2002). Ant-dispersed plants in temperate forests seem to have evolved relatively early blooming and seed release compared to species using other dispersal mechanisms, such as wind and birds (Thompson 1981 but see Ruhren & Dudash 1996; Handel & Beattie 1990; Oberrath & Boehning-Gease 2002; Gorb & Gorb 2003; Giladi 2006; Guitian & Garrido 2006) [Fig. 1, this study]. Myrmecochore seed set typically begins in conjunction with spring ant foraging and ends later in summer when preferred food sources (e.g. insects) become more available (Ruhren & Dudash 1996; Boulay *et al.* 2007; Clark & King 2012).

We used comparative analysis to investigate whether woodland myrmecochores in the eastern U.S. partition seed set timing based on seed size. As larger myrmecochore seeds generally have larger elaiosomes (Mark & Oleson 1996; Edwards, Dunlop & Rodgerson 2006), making them more attractive for ant foragers, we hypothesized that small-seeded plants fruit earlier in the season when ants are beginning to forage and that larger-seeded species fruit later when ant foragers are much more abundant. If this segregation results from competition for ant dispersers, as opposed to other mechanisms such as time for seed development, we posited that this segregation would not be observed for seeds dispersed by other mechanisms. We next employed direct field experiments to test whether the competitive strength of large seeds (*Asarum arifolium* Schreb. var. *acuta* (Pursh) Steyerm; hereafter, *Asarum*) and small seeds (*Anemone americana* Michx. Small; hereafter, *Anemone*) was consistent throughout the fruiting season. We placed seeds of both species in the same and in separate bait stations so that small and large

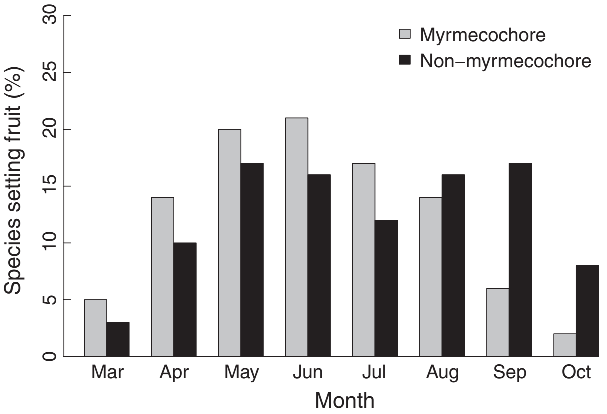

Fig. 1. Percentage of plants setting fruit by month for 36 myrmecochorous (ant-dispersed) and 36 non-myrmecochorous woodland perennial plant species. Seed phenology data were derived from Radford, Ahles and Bell (1968) for the Carolina region, U.S.

seeds were offered during and outside the times when they would naturally be available. We hypothesized that the presence of large seeds inhibits removal of small seeds, reflecting ant preferences for larger seeds (Hughes & Westoby 1992; Gorb & Gorb 1995; Ruhren & Dudash 1996; Garrido *et al.* 2002; Bas, Oliveras & Gomez 2009). If our comparative analysis and field trials revealed that seed size appears segregated temporally, which partitions ant dispersers as a resource, then we posited that the conceptualization of fundamental and realized niche requirements needs to be overhauled to include mutualist partners as a fundamental resource.

Materials and methods

SEED SIZE COMPARATIVE ANALYSIS

We used published seed size and phenology data to investigate whether plants segregate seed set during the growing season by seed size. Seed size was calculated as length × width, but 83% of the data lacked widths. When only seed length was given, we calculated seed size as length × ½ length. We used mean values when a range of seed lengths or widths was reported. We verified the veracity of our seed size estimates by comparing them with published seed mass data for some of the species from the Royal Botanic Garden Seed Information Database (SID 2008) and found a significant correspondence between estimated seed size and seed mass (Linear model: coeff. = 0.912, SE = 0.116, *t*-value = 7.876, *P*-value < 0.001, $R^2 = 0.61$).

We only used data referenced to the region that includes our field sites (described below) as seasonal phenology shifts with latitude. Approximately 36 plants in the region (see Appendix S1 in Supporting Information) use ants for seed dispersal (Handel 1976; Beattie 1978; Beattie, Culver & Pudlo 1979; Pudlo, Beattie & Culver 1980; Beattie & Culver 1981; Handel, Fisch & Schatz 1981; Gaddy 1986; Cain, Damman & Muir 1998; Mitchell, Turner & Pearson 2002). We relied on a single source (Radford, Ahles & Bell 1968) for seed set timing to avoid any confounding by climate variation, but we used additional sources for seed size (Weakley 2008; Flora of North America 2013; eFloras 2013). We also selected 36 non-myrmecochorous plants for comparison. In order to make the non-myrmecochorous species data set phylogenetically similar to the myrmecochore species data, we used an online phylogenetic data base (Stevens 2012) to select 36 non-myrmecochore, perennial, understorey species that were either in the same genus, family or order as the myrmecochore species, using the same seed set and size sources as used for myrmecochores. Importantly, our comparison species occur in similar habitats, assuring ecological similarity between the data sets for comparison; a condition that may be more important than phylogenetic controls in comparative analyses (Losos 2011).

In comparative analyses such as ours, where species (or genera) are treated as data points, there is a risk of the inclusion of non-independent data points whenever closely related species have similar trait values due to their relatedness rather than environmental response (Derrickson & Ricklefs 1988). Non-independent error violates the assumptions of statistical models that do not account for it and skews interpretation towards Type I error. Early blooming in myrmecochorous species does not appear to be phylogenetically autocorrelated (Oberrath & Boehning-Gease 2002), especially as ant-dispersed plants occur in the same families and genera as plants with other dispersal modes (see Appendix S1, this study; Thompson 1981; Oberrath & Boehning-Gease 2002). Still, several of the myrmecochorous species used here occur in the same genus or family so that correspondence between seed size and timing might be autocorrelated by taxonomy. To account for this potential bias, we used linear mixed models with plant phylogenetic distance as a random effect to correct for phylogenetic autocorrelation (Burns & Strauss 2011; Rafferty & Ives 2013) when evaluating seed set as a function of seed size for myrmecochorous and non-myrmecochorous plants. Phylogenies are unique, but statistically they resemble any spatial or temporal data set with replicates with interdependent error; data for which long-standing statistical methods exist (Ives & Zhu 2006; Dochtermann & Dingemanse 2013). The employment of linear mixed models for phylogenetic autocorrelated data is relatively new (Ives & Zhu 2006; Dochtermann & Dingemanse 2013; Rafferty & Ives 2013) but provides a suitable alternative to more traditional methods (e.g. Felsenstein 1985). We retrieved plant synonyms and taxonomic information with Nix (Kembel 2007) and used Phylomatic v3 (Webb & Donoghue 2005) to build phylogenetic trees. We calculated phylogenetic distance with the '*ape*' package (Paradis, Claude & Strimmer 2004) for the R statistical programming environment (R Development Core Team 2013). We fit the mixed models using the Laplace approximation in the '*lme4*' package (Bates *et al*. 2011) for R. The F-statistic is not considered accurate in mixed models; we used Markov chain Monte Carlo (MCMC) sampling (10 000 runs) in the '*language*' package (Baayen 2007) for R to estimate the coefficients and *P*-values for retained parameters in LMMs.

SEED BAIT STATION EXPERIMENTS

The study site was located in mature oak–hickory forest in the southern Appalachian Mountains of North Carolina, USA (35°17′ 10″ N, 85°17′27″ W, 777–790 m elevation). We established four plots (50 m apart) to offer *Anemone americana* (Ranunculaceae) and/or *Asarum arifolium* (Aristolochiaceae) seeds through the typical seed-set season for myrmecochores (March–June). At each plot, we placed three seed 'bait' stations spaced 1 m apart (4 plots x 3 bait treatments = 12 stations total). The 1-m bait-station spacing is about the maximum dispersal/foraging distance for *Aphaenogaster* ants so that adjacent bait stations should not have influenced ant decisions at any one bait station. Moreover, wild myrmecochore plant species co-occur at scales of a few cm (Cain, Damman & Muir 1998; Zelikova, Sanders & Dunn 2011; Gomez & Espadaler 2013; Warren & Bradford 2013) so the mixed-seed bait stations should represent the spatial scale of ant decisions where two myrmecochore species to drop seeds at the same time. The bait stations were 4 × 4 cm polystyrene weighing dishes secured into the soil with a 2-cm nail. The three bait-station treatments per plot were (i) five *Anemone* seeds, (ii) five *Anemone* + five *Asarum* seeds and (iii) five *Asarum* seeds. The baits were repeated 12 times from 15 March 2011, at weekly intervals. The seeds were loaded into the trays at 8 a.m. once per week and monitored for 120 min, sufficient time to determine the relative abundance and species frequency of ant foragers (Bestelmeyer *et al.* 2000; Ness, Morin & Giladi 2009). Bait visits are indicative of the proximity and abundance of ant colonies (Warren, Giladi & Bradford 2012).

Asarum produces consistently larger (Warren 2010; Warren & Bradford 2011) and higher quality seeds than *Anemone*. *Anemome* actually proffers an elaiosome mimic rather than an actual elaiosome (Pfeiffer, Huttenlocher & Ayasse 2009). The seeds produced by these two species span the gradient of typical myrmecochore seed sizes from the smaller-seeded, early season species (*Anemone*) to the larger-seeded, later-season species (*Asarum*) [see Appendix S1]. Because

Asarum sets seed much later (locally June) than *Anemone* (locally April), we could not use fresh diaspores to examine pairwise effects. Instead, we used previous-year seeds for the experiments. The seeds were collected in the region and stored frozen (−2 °C). Freezing myrmecochorous seeds does not appear to affect their efficacy in attracting seed-dispersing ants (Ness & Morin 2008; Clark & King 2012).

Whereas two-species comparisons often are discouraged because unmeasured interspecific differences may confound interpretation (Garland & Adolph 1994); seed characteristics other than size have little influence on removal rates by ants (Hughes & Westoby 1992); and the assumption that ants prefer larger seeds/elaiosomes is well-established (Hughes & Westoby 1992; Gorb & Gorb 1995; Ruhren & Dudash 1996; Garrido *et al.* 2002; Bas, Oliveras & Gomez 2009). Moreover, we used the seeds from the two plant species to test the consistency of competition throughout the fruiting season rather than examine species-specific adaptations.

ANT–SEED INTERACTION INDEX

A digital camcorder (Samsung SMX-F50BN) was positioned at each of the four mixed-seed bait stations to examine how seed removal patterns were related to ant interest in seeds and to measure ant foraging abundance. For each ant visit, we used the ant–seed interaction index developed by Culver and Beattie (1978) to score ant interest in seeds: (i) ignore – the ant pays no attention to the seed; (ii) antennate – the ant examines the seed with antennae; (iii) examine – the ant more thoroughly examines the seed (i.e. with mandibles); (iv) pickup – the ant attempts to move the seed; and (v) removal – the ant removes the seed from the treatment tray. In total, we reviewed 96 h of video footage and scored 210 ant visits for ant behaviour and species identity.

DATA ANALYSIS

We used autoregressive moving average (ARMA) models to analyse changes in the ant–seed interaction index and seed removal per ant (seeds ant^{-1}) by week. The ARMA models (Box, Jenkins & Reinsel 1994) account for autocorrelation between observations inherent in time-series analysis. We used Box–Jenkins ARMA models in the R statistical program (R Development Core Team 2013). The autoregressive portion of these models resembles a linear regression of the current time-series value against one or more previous values; the moving average is essentially a filtering function that compares the current value against random error in previous values (Shumway & Stoffer 2006). Generalized least squares (GLS) regressions with maximum likelihood were used to fit the models. The GLS model assumes that errors are correlated and may have unequal variances without assuming linearity in the data. We used the Durbin–Watson test implemented in the *car* package in R to determine the autocorrelation function (lag) for the ARMA models. We included second-order terms ($y = mx + mx^2 + b$) in the regression models to account for potential shifts in removal rates (i.e. curvilinearity) within the seasonal window (March–June).

Given that Warren, Bahn and Bradford (2011) and Warren and Chick (2013) show that minimum weekly spring temperatures best predict the foraging phenology of the dominant ant seed-disperser at our site (*Aphaenogaster* spp.), we analysed local weekly temperatures during the 12-week study period (http://www.ncdc.noaa.gov/cdo-web) from two nearby weather stations, Cullowhee, NC (35.3116°, −83.1747°; Elev. 668 m, 10 km from study site), and Franklin, NC (35.1802°, −83.3927°; Elev. 647 m, 16 km from study site). We used ARMA time-series models to investigate how foraging abundance corresponded with minimum temperatures and precipitation.

Results

SEED SIZE COMPARATIVE ANALYSIS

The 17 temperate forest myrmecochore genera used in the comparative analysis were spread across 15 different families. Myrmecochore seed set exhibited a unimodal pattern, peaking in May–July (Fig. 1). By comparison, early seed set was less common for the 30 non-myrmecochorous genera (16 families), and seed set for these species remained at similar levels in May–October (Fig. 1). Seed size increased significantly by month for myrmecochorous (coeff. = 0.997, *HPD95lower* = 0.686, *HPD95upper* = 1.759, *pMCMC* = 0.002) but not for non-myrmecochorous (coeff. = 0.024, *HPD95lower* = −1.493, *HPD95upper* = 1.927, *pMCMC* = 0.975) plant species (Fig. 2). Notably, many non-myrmecochorous species continued setting relatively small seeds late in the season, whereas the myrmecochores only set small seeds early in the season. The maximum size and mass for myrmecochore seeds were approximately 10 mm^2 (mean 4.7 mm^2) and 11.5 mg (mean 2.8 mg), respectively, and the range of seed sizes was small. Most non-myrmecochore seeds were not much larger (mean size 7.4 mm^2, mean mass 5.1 mg), but the range of seed sizes of non-myrmecochores was much wider and the seeds of two species were larger than 35 mm^2 and weighed more than 39 mg.

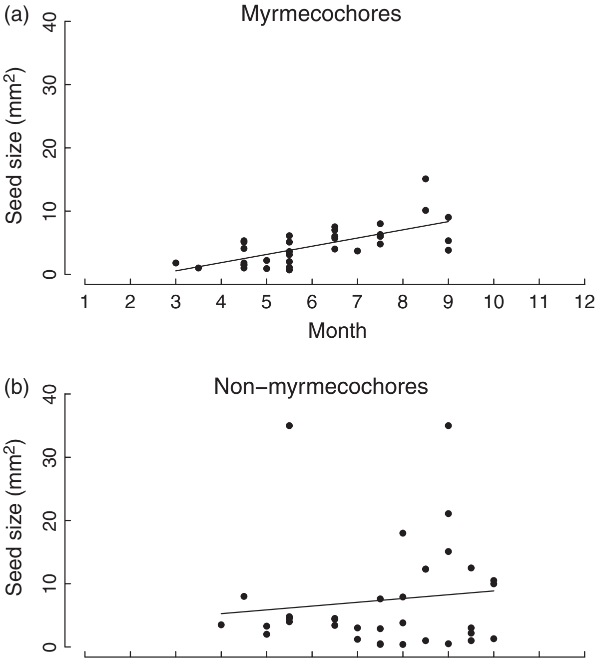

Fig. 2. Seed size as a function of seed set timing for 36 myrmecochorous (a) and 36 non-myrmecochorous (b) temperate forest, understorey, perennial plant species.

SEED REMOVAL RATES

Ants removed 15.8% of the 480 *Asarum* (large) seeds offered across the 12 weeks, with 10.2% from the *Asarum*-only treatment and 5.6% from the mixed *Anemone* + *Asarum* treatment. Of the 480 *Anemone* (small) seeds offered across the entire study period, 7.1% were removed by ants, most of which (6.5%) were from the *Anemone*-only treatment and only 0.6% from the mixed *Anemone* + *Asarum* treatment. The presence of the larger *Asarum* seeds in the bait station reduced *Anemone* seed removal to zero in all but one of the 12 study weeks (Fig. 3a,c), overall a 91% reduction. The presence of the smaller *Anemone* seeds also reduced ant retrieval of the larger *Asarum* seeds, but the reduction was less dramatic. When presented alone, weekly mean removal rates of *Asarum* seeds varied from 0% to 50% throughout the season, but maximum removal was capped at 20% in the presence of the smaller *Anemone* seeds (Figs 3b,d).

Anemone naturally drops its smaller seeds early in spring when ant dispersal is much less effective than later in the season when *Asarum* releases larger seeds. Specifically, during the late March/early April period when *Anemone* naturally drops seeds, ants collected 1.3% of the total offered seeds from *Anemone*-only treatments (Fig. 3). In contrast, they removed 17.5% of the total seeds from the *Asarum*-only treatments at this time. Later in the season, during the late May/early June period when *Asarum* naturally drops seeds, ants collected 13.8% of the total seeds from the *Anemone*-only treatments and 28.8% of the total offered seeds from the *Asarum*-only treatments (Fig. 3).

ANT BEHAVIOUR AND ABUNDANCE

In the mixed-species baits, we observed 210 ant visits across the 12 weeks. The predominant ants observed ($n = 154$, 73.4% of the total) were *Aphaenogaster picea* (Wheeler), and we restricted our behaviour assessments to this species, which is the key seed disperser at our sites (Warren, Giladi & Bradford 2010, 2012; Warren, Bahn & Bradford 2011) and the most abundant arthropod genera in eastern deciduous forests (King, Warren & Bradford 2013). Other ant species observed included *Tapinoma sessile* (12.3%), *Formica* spp. (7.8%) and *Camponotus* spp. (1.3%). The ant–seed interaction index (max. = 5) scored from the videography indicated that *A. picea* devoted significantly greater attention to *Asarum* (mean index = 2.48 ± 0.11 SE) than to the smaller *Anemone* (mean index = 2.09 ± 0.09) seeds during the March–June study period (t-test: $t = -2.597$, d.f. = 214, $P = 0.010$). Ant interest in the seeds, based on mean ant–seed interaction index scores, dropped significantly during the early weeks of the study (coeff. = −0.842, SE = 0.178, t-value = −4.726, $P = 0.002$) and then rose slightly (coeff. = 0.051, SE = 0.012, t-value = −4.133, $P = 0.004$) [Fig. 4a]. In contrast, ant abundance at the videography stations increased significantly (coeff. = 1.529, SE = 0.228, t-value = 6.693, $P < 0.001$) through the study period from approximately 3 ant h^{-1} during the late March/early April period (weeks 1–4), when *Anemone* naturally drops seeds, to approximately 16 ants h^{-1} during the early June period (weeks 11–12), when *Asarum* naturally drops seeds. At the same time, however, per capita seed removal dropped significantly (coeff. = −0.033, SE = 0.004, t-value = −8.751, $P < 0.001$), reflecting the fact individual ants increasingly removed fewer seeds [Fig. 4b].

Ant abundance varied significantly (coeff. = 1.212, SE = 0.276, t-value = 4.397, $P = 0.002$) with minimum temperature during the study period (Fig. 5) but showed no relationship with precipitation trends (coeff. = −0.473,

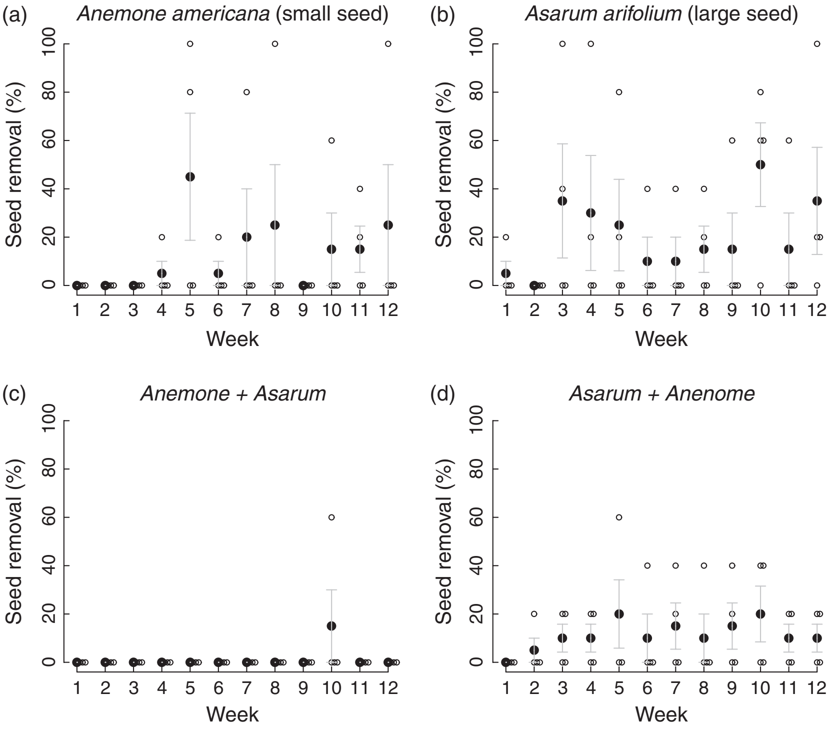

Fig. 3. Weekly seed removal (beginning 15 March 2011) for the small-seeded *Anemone americana* and large-seeded *Asarum arifolium* myrmecochores. Shown are the percentages of seeds removed weekly from four bait stations (data points are stacked) along with means (±SE). Seeds were offered individually by species (a, b) and in mixed-species (c,d) bait stations.

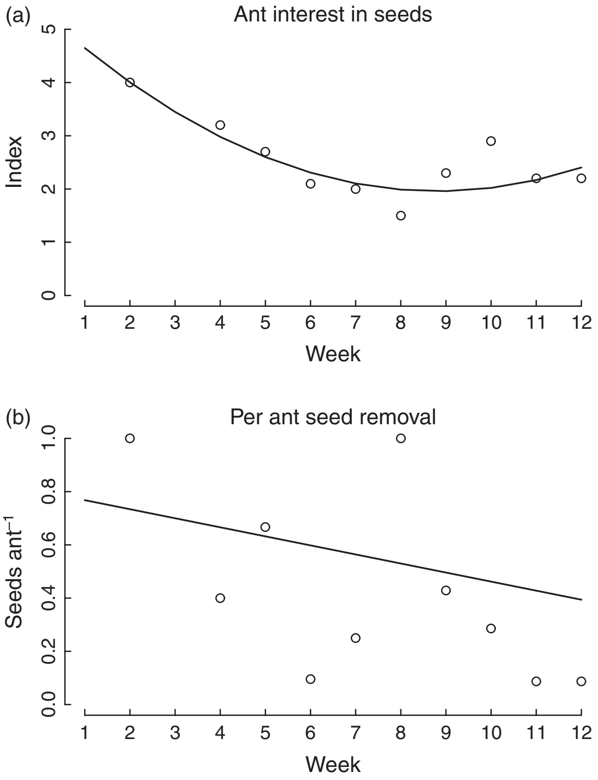

Fig. 4. Mixed-seed station observations of weekly ant interest in seeds based on an ant–seed interaction index (a) and per capita seed removal (b). The ant–seed interaction index indicates interest in offered seeds, with a minimum = 0 (ignore) and maximum = 5 (seed removed).

SE = 0.621, *t*-value = −0.762, $P = 0.468$), and there was no temperature x precipitation interaction (coeff. = 0.049, SE = 0.082, *t*-value = 0.598, $P = 0.566$). Few ants foraged in weeks 2 and 8 when minimum temperatures dropped below 2 °C, and none removed seeds during weeks 1 and 3 when minimum temperatures dropped to 0 °C.

Discussion

Strong competitors get the goods, often pushing poor competitors towards the lower end of resource gradients (e.g. Connell 1980). We show that seed set in eastern N.A. myrmecochores appears staggered by size so that poor competitors drop their smaller seeds in early spring when the larger seeds of strong competitors are scarce. We used small- and large-seeded myrmecochorous plants to demonstrate the competitive mechanism experimentally: the presence of large seeds greatly inhibits the removal of small seeds that would otherwise be retrieved by ants. The comparative literature analysis and field experiments together suggest that species compete for dispersal mutualists, indicating that ants are a fundamental resource for myrmecochorous plants.

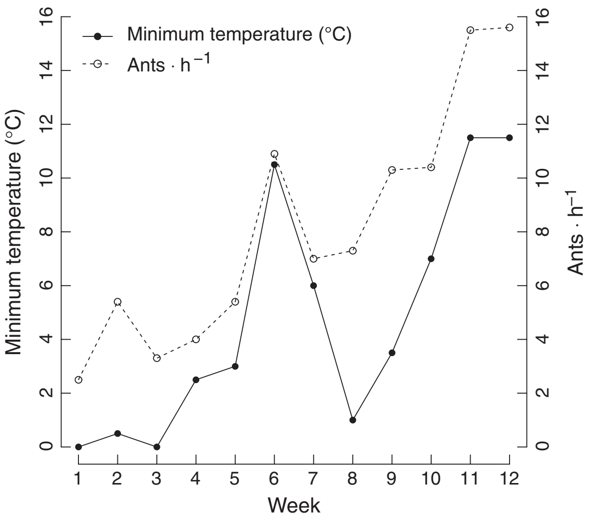

Fig. 5. Weekly minimum temperature (°C) and ant visits hour^{-1} at mixed-seed bait stations.

DISPERSAL WINDOW

A distinct seed-dispersal window is believed to exist for myrmecochores between early spring, when ant foraging activity is limited (Beattie & Culver 1981; Giladi 2006; Warren, Bahn & Bradford 2011; Clark & King 2012), and later in the season when alternate food sources for ants become increasingly available (Carroll & Janzen 1973; Gorb & Gorb 2003; Boulay *et al.* 2005; Guitian & Garrido 2006). We observed that ant foraging was minimal in early spring when minimum temperatures are lowest, resulting in sporadic seed removal. Early spring also is when small-seeded myrmecochores typically set seed. When larger seeds were artificially released early, however, they were retrieved at higher rates than the smaller seeds, and they inhibited retrieval of the small seeds. Conversely, artificially releasing smaller seeds later in the season (when larger-seeded myrmecochores typically set seed) increased their retrieval by ants (but only in the absence of the larger seeds). Similarly, Ruhren and Dudash (1996) found that delaying *Erythronium americanum* seeds – an early blooming myrmecochore with seeds of similar size to *Anemone* – a month after the natural window increased seed removal rates. These results suggest that small-seeded myrmecochores would increase seed dispersal by delaying seed set if they did not have to compete with larger-seeded myrmecochores.

Aphaenogaster picea was the dominant ant at our seed stations, and visitation rates increased more than fivefold between March and June; however, even though visitations increased, individual ant interest in the seeds dropped significantly after the first 6 weeks. As spring turned to summer, the ants spent less time investigating the seeds (either through attenuation or manipulation), and fewer seeds were removed per foraging ant. Overall, however, seed removal did not drop precipitously in early summer because there were many more ants actively foraging, compensating for the lessened interest. Our data appear consistent with the idea that myrmecochores release seeds relatively early, compared to non-myrmecochorous species as an adaptation that maximizes on ant interest early in the growing season (Thompson 1981 but see Ruhren & Dudash 1996; Handel & Beattie 1990; Oberrath

& Boehning-Gease 2002; Gorb & Gorb 2003; Giladi 2006; Guitian & Garrido 2006). However, the mechanism behind the adaptation appears more nuanced. That is, our data additionally suggest that small-seeded species are forced through competition for ants by larger-seed species into the poor end of the resource gradient (i.e. early spring when ant foragers are scarce). The pushing of seed set of smaller-seeded species earlier emphasizes the difference in timing of seed release between myrmecochores and non-myrmecochores. Myrmecochore seed dispersal then appears to be under a hierarchical set of controls that select for early season seed set. First, myrmecochore seeds must compete for ants with alternate food resources, which become abundant later in the growing season. Secondly, within the myrmecochore guild, smaller myrmecochorous seeds are less competitive than larger seeds at attracting ant dispersers, forcing smaller-seeded species to set seeds even earlier. Competition pressure within dispersal mutualist guilds seems a likely force shaping partner evolution (Palmer, Stanton & Young 2003).

SEED COMPETITION

In direct, pairwise competition experiments conducted throughout the growing season, we found substantial evidence for seed competition. The presence of the larger *Asarum* seeds essentially eliminated (91% reduction) any *Anemone* seed dispersal. The only *Anemone* seed removal in the presence of *Asarum* occurred once late in the season when the plant would otherwise not naturally release seeds. Interestingly, *Asarum* seed removal also decreased (46%) in the presence of *Anemone* seeds, which appears a muting of major removal events rather than an overall decline in background seed removal rates. This effect may be because the ants become seed saturated (Smith *et al.* 1989), or because the presence of *Anemone* seeds dilutes the perceived quality of the bait resource.

More than a dozen ant species will occasionally pick up woodland herb seeds, but only 2–4 *Aphaenogaster* species dominate seed removal in eastern N.A. deciduous forests (Ness, Morin & Giladi 2009; Warren, Giladi & Bradford 2010). Such specialization is consistent with competition for mutualist partners which might select for a subset of available partners with specialized adaptations for the mutualism (Palmer, Stanton & Young 2003). Competition for dispersers might then be expected to drive all myrmecochore species towards an increasing seed size, but larger seed size also increases attractiveness to seed predators (Janzen 1969; Heithaus 1981) and might outsize ant mandible gape (Gomez, Espadaler & Bas 2005). Moreover, dispersal mode in itself is not likely a strong evolutionary driver of seed size (Leishman 2001; Moles & Westoby 2004; Moles 2005), though myrmecochore seed size generally is less variable than for non-myrmecochores (Moles *et al.* 2005). Indeed, dispersal mode is postulated to exert more pressure on the timing of seed release, particularly in ant-dispersed plants (Beattie & Culver 1981; Handel, Fisch & Schatz 1981; Heithaus 1986; Smith *et al.* 1989; Ruhren & Dudash 1996). We therefore suggest that competition for ant dispersers seems the most plausible mechanism for sorting seed release phenology so that small-seeded myrmecochores set early to avoid competition with large-seeded myrmecochores.

ALTERNATE EXPLANATIONS FOR MYRMECOCHORE SEED RELEASE TIMING AND SIZE

Researchers typically associate early spring flowering with pollinators rather than dispersers (Cruden, Hermann & Peterson 1983; Kevan & Baker 1983), which could then explain why myrmecochores generally set seed earlier than non-myrmecochores. However, although early blooming may reduce competition for pollinators (Schemske 1978; Schemske *et al.* 1978; Motten 1982; Campbell & Motten 1985), there is no indication that myrmecochores suffer pollinator limitation with delayed blooming. Early flowering plants, mostly myrmecochores, do not produce specific floral traits associated with early season pollinators (Oberrath & Boehning-Gease 2002), and at least 40 insect pollinators (e.g. solitary bees, thrips, flies, beetles) visit myrmecochores in the *Asarum* and *Anemone* genera (Wyatt 1955; Bernhardt 1976; Murphy & Vasseur 1995; Libby, Murrell & Carroll 1996). Earlier-fruiting myrmecochores also might have smaller seeds because they have less time for resource acquisition, but non-myrmecochores produce small seeds throughout the season whereas myrmecochores only do at the start of the season. Furthermore, reproduction in many understorey herbs (including myrmecochores) is strongly influenced by carbon storage from the previous, not current, year (Nault & Gagnon 1988; Snow & Whigham 1989; Stowe *et al.* 2000; Stancato, Mazzafera & Buckeridge 2001).

Conclusions

Evidence that plants compete for dispersal services upholds the importance of competition in niche theory, but it undermines a strict abiotic versus biotic niche dichotomy. Hutchinson envisioned all abiotic niche requirements along axes in an *n*-dimensional hypervolume with access to those resources limited by competition with other species (Hutchinson 1957). Pulliam (2000) suggested a model that eliminates the fundamental versus realized dichotomy by suggesting the niche comprises all of the requirements needed for population persistence, both abiotic and biotic. Our results support this perspective as biotic interactions with ants seem fundamental to the myrmecochore niche – as does other work demonstrating myrmecochore dependence on ant dispersers (Kalisz *et al.* 1999; Warren, Giladi & Bradford 2010; Rodriguez-Cabal, Barrios-Garcia & Nunez 2012; Warren & Bradford 2013) – where myrmecochores must compete for ants as they do for abiotic resources. The availability of the ant mutualist therefore forms a niche requirement axis alongside standard niche factors such as light and soil moisture.

Competition for mutualists appears to drive niche segregation among myrmecochorous seeds by size and timing. Specifically, our results suggest myrmecochorous plants segregate the timing of seed set based on the competitive stature of their propagules. Small-seeded species release seeds during early spring, a period where ants show the greatest interest in myrmecochore seeds, but exhibit weak and inconsistent foraging (due to low minimum temperatures and lower ant abundance). Larger-seeded species produce a resource more attractive to the ants (which favour it over smaller seeds) and set them later in spring when ant foragers are less interested but highly abundant. Long-standing and developing theory in ecology generally focuses on biotic interactions for resources as either negative or positive (but see Callaway & Walker 1997; Bronstein 2009). Our data suggest that plants compete for mutualists, demonstrating how negative and positive interactions can jointly structure animal–plant mutualisms.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Plant species used for seed size and phenology analysis.