

# Competition does not come at the expense of colonization in seed morphs with increased size and dispersal<sup>1</sup>

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**PREMISE OF THE STUDY:** Seed-level trade-offs of heterocarpic species remain poorly understood. We propose that seedlings emerging from seeds with a permanent pappus (dispersing seeds) are stronger competitors than those emerging from seeds without a pappus (nondispersing seeds) because dispersing seeds are larger and germinate faster than nondispersing seeds in *Centaurea solstitialis*.

**METHODS:** We conducted a competition experiment with both seed morphs, in which we recorded emergence rate and proportion, estimated seed dispersal by wind (anemochory) and by mammals (exozoochory), and measured size and abundance of seed morphs.

**KEY RESULTS:** We found that seedlings from pappus seeds had greater competitive abilities than those from non-pappus seeds. Similarly, pappus seedlings emerged at much faster rates and larger proportions than non-pappus seedlings. Pappus seeds were larger, were more numerous, and displayed improved exozoochory compared to non-pappus seeds. Anemochory was poor for both seed morphs.

**CONCLUSIONS:** We found support for our hypothesis, raising in turn the possibility that competition and colonization are positively associated in seed morphs of heterocarpic species with enhanced exozoochory of larger seeds. These findings are not consistent with those from heterocarpic species with enhanced anemochory of smaller seeds or slower-germinating seeds. Our results additionally suggest that pappus and non-pappus seeds of *C. solstitialis* display a task-division strategy in which pappus morphs colonize and preempt unoccupied sites through improved dispersal and fast and large emergence of seedlings with increased competitive abilities, whereas non-pappus morphs promote site persistence through delayed germination and dormancy. This strategy may contribute to the success of *C. solstitialis* in highly variable environments.

**KEY WORDS** anemochory; bet-hedging; *Centaurea solstitialis*; competition; dispersal; dormancy; exozoochory; heterocarpy; life history traits; seed size

Organisms have evolved myriad strategies to cope with the broad variation in biotic and abiotic conditions they experience (Grime and Pierce, 2012). Central to adapting to diverse and dynamic

environments are trade-offs in which increased survival and reproduction (fitness) under certain conditions come at the expense of decreased fitness under other conditions (Grime, 2001). Trade-offs expose adaptive limitations of organisms and set the path for ecological specialization (Grime and Pierce, 2012). Classic examples of broad trade-offs include constraints to simultaneously growing and defending (Herms and Mattson, 1992), germinating and remaining dormant (Cohen, 1966), and competing and colonizing (Grime, 1974; Tilman, 1994). The outcomes of those trade-offs are expected to be selected for, depending on herbivore pressure, environmental predictability, and disturbance frequency, respectively. Understanding how organisms solve adaptive dilemmas has shed light on the determinants of species abundances and distributions (Bonsall et al., 2004; Adler et al., 2005; Ridenour et al., 2008; Viola et al., 2010; Kempel et al., 2011; Lind et al., 2013).

Some plant species, notably within the Asteraceae, produce single-seeded fruits with two morphologies, a type of heterocarpy

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commonly known as seed dimorphism (Imbert, 2002). In addition to differing in appearance, seed morphs can differ in function (reviewed by Imbert, 2002), including dispersal (Venable and Levin, 1985a; Venable et al., 1987; Imbert, 1999; Mandák and Pysek, 2001; Cheptou et al., 2008), germination rate and dormancy (Venable and Levin, 1985a; Venable et al., 1995; Cheplick, 1996; Hierro et al., 2009; Baskin and Baskin, 2014; Bhatt and Santo, 2016), seedling growth and survival (Cheplick and Quinn, 1982; Venable and Levin, 1985b; Cheplick and Grandstaff, 1997; Cheplick and Sung, 1998; Lerner et al., 2008), and seedling competition (Weiss, 1980; Cheplick and Quinn, 1982; Cheplick and Quinn, 1983; Venable, 1985a; Imbert et al., 1997; Cheplick and Wickstrom, 1999). Research assessing interdependence between those functions has largely focused on examining the theoretical expectation that dispersal in space and time (dormancy) correlate negatively (Venable and Lawlor, 1980; McEvoy, 1984; Venable and Levin, 1985a; Olivieri, 2001; Vitalis et al., 2013; reviewed by Baskin and Baskin, 2014; Buoro and Carlson, 2014; Rubio de Casas et al., 2015). In a recent breakthrough, Dubois and Cheptou (2012) explored an alternative trade-off and showed that seedlings of *Crepis sancta* emerging from seeds with high wind-dispersal abilities (anemochory) were weaker competitors than those emerging from seeds with low dispersal. Consequently, seed morphs were proposed to be subject to the classic competition–colonization trade-off (Dubois and Cheptou, 2012). In addition, differences in competition appeared to be mediated by germination phenology, given that nondispersing seeds germinate earlier than dispersing ones, conferring a competitive advantage. Interestingly, dispersing and nondispersing seeds in *C. sancta* exhibit no dormancy and no variation in endosperm size. A negative correlation between competition and colonization can also be expected, however, in heterocarpic species with anemochory that do vary in seed size, because smaller (lighter) seeds commonly display increased dispersal but produce seedlings with decreased competitive abilities (Weiss, 1980; Cheplick and Quinn, 1982; Imbert et al., 1997; Cheplick and Wickstrom, 1999; but see Venable, 1985a). Rather than size, the presence of permanent dispersal structures likely plays a key role in animal dispersal of seeds (exozoochory; Baskin and Baskin, 2014). Heterocarpic species with differences in seed size and exozoochory may consequently exhibit an association between competition and colonization different from that previously reported. Heterocarpic species provide suitable models for studying trade-offs (Rubio de Casas et al., 2015); however, the nature of the association between different functional roles within different seed morphs remains poorly understood (Buoro and Carlson, 2014).

*Centaurea solstitialis* L. (yellow starthistle; Asteraceae) is an annual ruderal (i.e., weed), native to Eurasia and globally distributed (Eriksen et al., 2014), that produces two types of seeds (technically, achenes). Peripheral, outer seeds are smaller, darker, and do not have a pappus; whereas central, inner seeds are larger, cream-colored, and bear a permanent pappus (Maddox et al., 1985; Olivieri and Berger, 1985; Joley et al., 1997). In contrast to other Asteraceae species, in which the pappus facilitates anemochory (e.g., Venable and Levin, 1985a; Cheptou et al., 2008), the pappus of *C. solstitialis* is thought to favor exozoochory. The pappus appears to be too small in relation to the mass of the seed to provide anemochory (Roché, 1992). Assessments of wind dispersal in the species showed that, in fact, seeds from both morphs fell within 0.30 m from the mother plant (Roché, 1992). We are not aware of estimates of exozoochory for *C. solstitialis*. The species has a high reproductive output, and

pappus seeds are five times more numerous than non-pappus seeds (Benefield et al., 2001; Uygur et al., 2004). Limited wind dispersal and high fecundity suggest that plants from both pappus and non-pappus seeds are exposed to strong intraspecific competition. In central Argentina, seed morphs also vary in size and germination rate and proportion (i.e., dormancy), such that pappus seeds are larger (Hierro et al., 2013), germinate faster, and exhibit smaller proportions of dormant seeds (Hierro et al., 2009) than non-pappus seeds. Assuming that the pappus indeed enhances dispersal, dimorphic seeds in populations of Argentina comply with the dispersal–dormancy trade-off (Snyder, 2006; Buoro and Carlson, 2014; Rubio de Casas et al., 2015).

Here, we explore the competition–colonization trade-off in seed morphs of Argentinean populations of *C. solstitialis*. Because seed size (Rees and Westoby, 1997; Cheplick and Wickstrom, 1999; Graebner et al., 2012) and germination rates (Donohue et al., 2010; Gioria and Pysek, 2017) can influence the outcome of competition and the pappus is likely to improve dispersal, we propose that competitive ability does not trade off with colonization ability within the dimorphic seeds of *C. solstitialis*. If our hypothesis is correct, pappus seeds will produce stronger competitive seedlings and display increased dispersal abilities compared to non-pappus seeds. To test our hypothesis, we conducted a competition experiment with pappus and non-pappus seeds in the greenhouse and measured seed dispersal in the field.

## MATERIALS AND METHODS

**Study site**—Field activities for this study were conducted in sites surrounding Santa Rosa, La Pampa, Argentina (36°35′30.86″S, 64°16′45.98″W). The region is located within the Caldén District (commonly known as Caldenal), a semiarid, open forest dominated by the tree *Prosopis caldenia* (Cabrera, 1994). Other common woody species include the shrubs *Condalia microphylla*, *Geoffroea decorticans*, and *Schinus fasciculatus*. Perennial bunchgrasses dominate the understory, including *Piptochaetium napostaense*, *Poa ligularis*, and *Nassella* spp. Soils are sandy, and the climate is continental (Cano et al., 1980). Precipitation occurs mainly as rain from October to March (i.e., spring and summer months in the Southern Hemisphere) and exhibits broad interannual variation, particularly in winter (Hierro et al., 2009)—a crucial period for the establishment of *C. solstitialis* seedlings, because seeds germinate in the fall (Hierro et al., 2013). Mean annual precipitation and temperature for Santa Rosa are 641 mm (1911–2015; G. Vergara, National University of La Pampa, unpublished data) and 15.4°C (1941–1990; <http://www.worldclimate.com>).

**Competition experiment**—Seeds for the competition experiment were collected from five populations of *C. solstitialis* and five populations of *Bromus catharticus* var. *rupestris* (formerly *B. brevis*; hereafter *Bromus*), a native annual grass common in the Caldenal (Rúgolo de Agrasar et al., 2005), in December 2008–January 2009. Populations of both species were located in and near Santa Rosa and were separated from each other by a minimum distance of ~5 km (Appendix S1; see Supplemental Data with this article). Seeds were collected from 30 individuals per population and pooled into a single sample per species. From the pool, seeds that looked healthy and filled with an embryo were selected for the experiment. A viability test was conducted on seeds of each morph by submerging halves of

100 pappus and 100 non-pappus seeds in tetrazolium solution in Petri dishes (Cottrell, 1947). The mass of 50 pappus and 50 non-pappus seeds was also recorded. In addition, the mass of the endosperm and embryo was obtained after cutting seeds longitudinally and removing the seed coat. Finally, the seed-coat thickness of 50 pappus and 50 non-pappus seeds was measured by cutting seeds longitudinally in halves and placing one of them under a microscope.

The experiment was conducted in the greenhouse of the Agronomy Department at the National University of La Pampa, located 10 km from Santa Rosa. The greenhouse was not climate controlled, and the timing of the experiment matched the natural emergence time of the species in central Argentina. The experiment ran for 120 d from early April to August 2009. Plants were grown in 800 mL plastic pots filled with a mixture of natural caldenal soil and fine sand in a 3:1 proportion. Soil was passed through a 710  $\mu\text{m}$  mesh sieve to remove seeds. The competitive performance of seedlings emerging from pappus and non-pappus seeds was assessed in intramorph, intermorph, and interspecific treatments. In the intramorph treatment, pots were sown with either pappus or non-pappus seeds. In the intermorph treatment, pots were sown with a mixture of both pappus and non-pappus seeds. In the interspecific treatment, *Bromus* was sown with either pappus or non-pappus seeds. Interspecific competition is likely to be common and strong for seedlings emerging from seed morphs dispersed away from the mother plant. For each treatment, seeds were added at four densities: 1, 2, 10, and 20 seeds per pot. In the intermorph and interspecific treatments, different seed types were added in a 50:50 proportion (Lortie et al., 2009). For the treatments with densities 1 and 2,  $n = 13$ ; for the treatments with densities 10 and 20,  $n = 5$ . Replication differed between density levels because we expected higher variation in seedling size and competition strength for low than for high densities. Five pots received no seeds to assess the efficacy of the soil-sieving procedure. The total number of pots in this experiment was 159.

To identify seedlings emerging from either pappus or non-pappus morphs, seeds in pots were sown in a 0.5 cm wire grid of cells placed on top of the soil, with cells randomly assigned to be colored blue or red. Pappus and non-pappus seeds were planted in blue and red cells, respectively. After sowing, pots were watered to field capacity to promote seedling emergence. Thereafter, seedlings were watered as needed, as determined by daily visual inspections. No fertilizer was added. To maintain treatment densities, seeds previously germinated in Petri dishes were added to pots in which individuals did not emerge 10 d after the first watering (i.e., a controlled-density series replacement). Seedlings from the initial sowing that emerged after those 10 d were removed from pots. Emergence was recorded for 61 d, and from these data both final proportional emergence (number of seedlings emerged/number of seeds added) and emergence rates (Timson's index,  $\Sigma n$ , where  $n$  is the cumulative emergence proportion at each sampling date; Timson, 1965; Baskin and Baskin, 2014) were estimated. At the end of the experiment, the aboveground biomass of all plants was harvested and dried in a laboratory oven at 60°C to constant weight. Biomass data were used to calculate relative interaction indexes (RIIs) for the different competition treatments, according to the following equation (Armas et al., 2004):

$$\text{RII} = (B_w - B_0) / (B_w + B_0)$$

where  $B_0$  is the biomass of the target plant when growing alone and  $B_w$  is that of the target plant when growing with other plants. RII ranges from  $-1$  to  $1$ , with negative values indicating competition and positive values facilitation. In our study,  $B_w$  was the aboveground biomass of every single seedling grown with neighbors, whereas  $B_0$  was the mean aboveground biomass of the 13 seedlings grown alone that resulted from pappus and non-pappus seeds of *C. solstitialis* and seeds of *Bromus*.

**Estimates of seed-morph abundance**—The numbers of pappus and non-pappus seeds per capitula were estimated by sampling 20 individuals in each of five populations, with the exception of one population, in which 30 individuals were sampled. Capitula were sampled in January 2010, coinciding with the peak flowering and fruiting time of the species in central Argentina. Populations were located at the same sites as those used for seed collections in the competition experiment. *Centaurea solstitialis* opens capitula and readily disperses seeds at maturation. To avoid seed loss, capitula were bagged using  $0.06 \times 0.09$  m cotton bags once inflorescences turned color from bright to pale yellow, indicating the end of pollination. One capitulum per individual was bagged. At seed maturation,  $\sim 2$  wk after bagging, capitula were collected and the numbers of pappus and non-pappus seeds present in each of them were determined.

**Dispersal estimates**—Estimations of dispersal abilities of pappus and non-pappus seeds were performed by studying the two main modes of passive dispersal in *C. solstitialis*, exozoochory and anemochory (Roché, 1992). To assess exozoochory, pelts of three common mammal species in the Caldenal, the European hare (*Lepus europaeus*), pampean gray fox (*Lycalopex gymnocercus*), and Patagonian skunk (*Conepatus humboldtii*), were passed through five *C. solstitialis* populations along a 100 m transect at each population. These populations were the same as those used for collecting seeds for the competition experiment. Exozoochory sampling was conducted monthly from the onset of seed release in the summer of 2009 (January) to plant senescence in the winter of the same year (July). Sampling took place in areas that were not used for seed collections. In the laboratory, pappus and non-pappus seeds were detached from pelts with a comb and counted. Seeds from all three pelts were combined into a single sample and grouped by season for each population. Anemochory, in turn, was studied by placing seed traps (8 cm diameter  $\times$  10 cm height) at ground level at increasing distances from the border of the five *C. solstitialis* populations used to assess exozoochory (Roché, 1992). These measurements were made in areas not affected by other sampling. Four transects were placed at each population, except for one, where only three transects were located because of terrain restrictions. Along each transect, a seed-trap pair, with traps in the pair separated by 5 cm, were inserted into the ground at 0 m, 1 m, 2 m, 4 m, 8 m, 16 m, and 32 m from the population border. As before, seeds in traps were collected monthly from January 2009 to July 2009 and counted. Seeds from trap pairs at each distance were combined into a single sample and grouped by season.

**Data analyses**—Differences in complete seed mass, endosperm plus embryo mass, and seed-coat thickness between pappus and non-pappus morphs were assessed with  $t$ -tests. All other comparisons were conducted with generalized linear mixed models (GLMMs) that

assumed a binomial distribution and logit link function for proportions (emergence rate and percentage), normal distributions and identity link functions for linear response variables (RII), and Poisson distributions and log link functions for count variables (number of seeds). In addition, analyses over time (dispersal) were conducted with repeated-measures generalized linear models (GLMs; exozoochory) and GLMMs (anemochory). Significance values of pairwise comparisons were adjusted with the Bonferroni procedure. The model used to analyze emergence rates, emergence proportions, and RIIs of *C. solstitialis* seedlings in the competition experiment considered seed morph, competition treatment, density, and all two- and three-way interactions as fixed factors and pot as a random factor. In addition, the model that analyzed the same dependent variables for *Bromus* seedlings included seed morph, density, and their interaction as fixed factors and pot as a random factor. Differences between the numbers of pappus and non-pappus seeds in each capitula were evaluated with a model in which seed morph was considered as a fixed factor and capitula (population) as a random factor. Finally, for exozoochory data, populations entered the model as subjects, sampling time as repeated measures, and seed morph, sampling time, and their interaction as fixed factors. Similarly, in the model used to compare anemochory between pappus and non-pappus seeds, seed traps were considered as subjects; sampling time as the repeated measures; seed morph, sampling time, distance from the population border, and all possible two- and three-way interactions as fixed factors; and transect (population) as a random factor. To deal with problems linked to datasets with large numbers of zeros and to conduct all possible comparisons and interactions, the number of seeds collected in traps + 1 was the dependent variable. Analyses were performed with Sigma Plot (*t*-tests) and IBM SPSS Statistics 22 (GLMMs and GLMs).

## RESULTS

**Competition experiment and seed-morph abundance**—*A. Viability, mass, seed-coat thickness, and abundance of seeds*—Estimated viability from tetrazolium tests was high for both pappus (100%) and non-pappus (98%) seed samples used in the competition experiment. Consequently, seeds that did not germinate (i.e., non-emerging seedlings) in the competition experiment were considered to be dormant. The mass of pappus seeds was >40% larger than that of non-pappus seeds (Table 1). Similarly, the endosperm and embryo were 25% larger in pappus seeds than in non-pappus seeds. Seed morphs did not differ, however, in seed-coat thickness. Pappus seeds were over five times more abundant than non-pappus seeds in *C. solstitialis* capitula. To account for the departure from a 1:1 proportion in the abundance of pappus and non-pappus seeds in capitula, the number of pappus seeds was divided by 5.439 (see Table 1) in the exozoochory estimates, and analyses were conducted with the corrected data.

*B. Rate and proportion of seedling emergence*—Seedlings from pappus seeds emerged >40% faster than those from non-pappus seeds in the three competition treatments (Fig. 1). In addition, the emergence of *C. solstitialis* seedlings was >20% more rapid when the same seed morphs grew together than when they were planted with the seeds from the other morph or *Bromus* ( $P < 0.001$  for all pairwise comparisons). There were no significant differences between the two latter treatments ( $P = 0.551$ ). The emergence rate of seedlings was maximum at the lowest manipulated density ( $P < 0.05$ ), and it decreased from density 20 to density 2 ( $P < 0.050$  for all pairwise comparisons). In turn, the emergence rate of *Bromus* seedlings in pots with pappus seeds was similar to that in pots with non-pappus seeds ( $P = 0.148$ ).

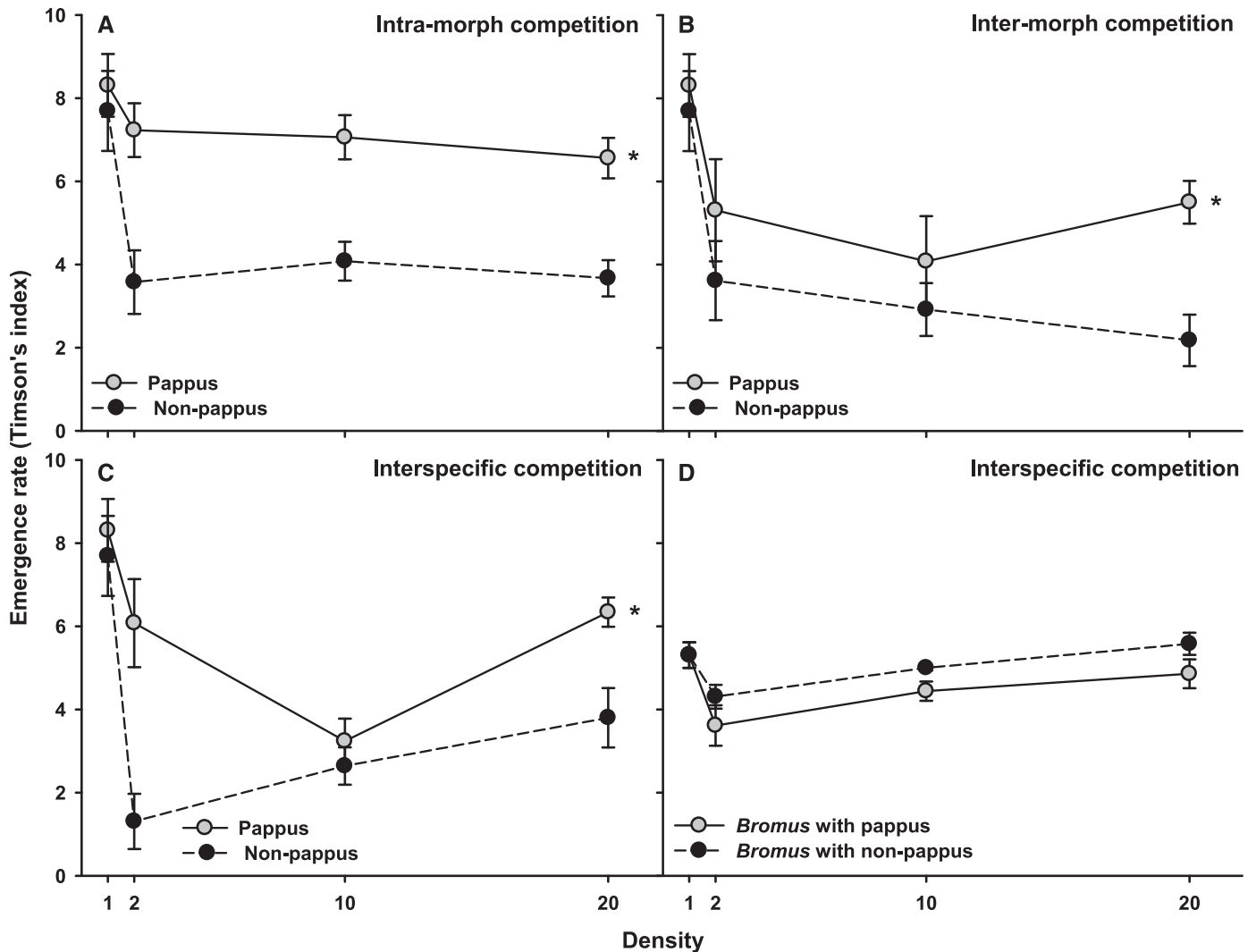
The proportion of seedlings that emerged from pappus seeds was nearly 20% and 35% larger than that of seedlings from non-pappus seeds in the intramorph and interspecific competition treatments, respectively (Fig. 2). In the intermorph treatment, significant differences between seed morphs were observed only at the highest density ( $P < 0.001$ ). In addition, emergence proportions were greater at the lowest-density treatment than at any other density ( $P < 0.010$ ), which showed no statistical differences between each other ( $P > 0.500$  for all pairwise comparisons). The proportion of *Bromus* seedlings that emerged in pots with pappus seeds was similar to that in pots with non-pappus seeds ( $P = 0.537$ ).

*C. Interaction-intensity estimates*—Competitive effects of pappus seedlings on the aboveground biomass of both non-pappus and *Bromus* seedlings were stronger than the effects of non-pappus seedlings on pappus and *Bromus* seedlings (Fig. 3 and Table 2). There were no differences in the intensity of competition between seedling types in the intramorph treatment ( $P > 0.05$ ). Also, competitive interactions were stronger in both the intramorph and intermorph treatments ( $P > 0.05$  for the pairwise comparison between those treatments) than in the interspecific treatment ( $P \leq 0.005$  for both pairwise comparisons). *Bromus* seedlings exerted stronger negative effects on the biomass of non-pappus seedlings than on that of pappus seedlings ( $P < 0.001$ ). Seedling density greatly increased competitive effects on both *C. solstitialis* and *Bromus* seedlings ( $P < 0.001$  for all of pairwise comparisons).

*Dispersal estimates*—*A. Exozoochory*—In summer, at the peak of fruit production in *C. solstitialis*, after abundance correction, pappus seeds were over five times more abundant than non-pappus seeds in mammal pelts ( $P < 0.001$ ), but no statistical differences were detected between seed-morph numbers in autumn and winter ( $P = 0.127$  and  $P = 0.543$ , respectively;  $F_{\text{Seed morph}} = 5.419$ ,  $df = 2$  and  $24$ ,  $P = 0.029$ ;  $F_{\text{Time}} = 25.468$ ,  $df = 2$  and  $24$ ,  $P < 0.001$ ;  $F_{\text{Seed morph} \times \text{Time}} = 5.751$ ,  $df = 2$  and  $24$ ,  $P = 0.009$ ; Fig. 4). Exozoochory in pappus seeds was at a maximum also in the summer, and it steadily decreased as the year progressed ( $P < 0.001$  for all pairwise comparisons). For non-pappus seeds, exozoochory did not differ between summer

**TABLE 1.** Mass, seed-coat thickness, and abundance of pappus and non-pappus seeds (number of seeds per capitulum) of the Argentinean populations of *Centaurea solstitialis* used in this study. Data are means  $\pm$  SD of 50 seeds (mass and seed-coat thickness) and 20 capitula (one per plant) in each of four populations and 30 capitula in one population (abundance).

Variable	Pappus	Non-pappus	Statistic	P
Seed mass (g)	$1.982 \times 10^{-3} \pm 0.298 \times 10^{-3}$	$1.404 \times 10^{-3} \pm 0.269 \times 10^{-3}$	$t_{98} = 10.183$	<0.001
Endosperm and embryo mass (g)	$7.160 \times 10^{-4} \pm 2.170 \times 10^{-4}$	$5.740 \times 10^{-4} \pm 1.600 \times 10^{-4}$	$t_{98} = 3.723$	<0.001
Seed-coat thickness ( $\mu\text{m}$ )	$71.484 \pm 14.954$	$74.266 \pm 15.616$	$t_{98} = -0.910$	0.365
Abundance	$56.350 \pm 10.824$	$10.361 \pm 1.725$	$F_{1,218} = 2811.291$	<0.001



**FIGURE 1** Emergence rate of *Centaurea solstitialis* seedlings derived from pappus and non-pappus seeds in the intramorph (A), intermorph (B), and interspecific competition treatments (C). Emergence rate of *Bromus catharticus* var. *rupestris* (*Bromus*) (D) is shown for the interspecific treatment. In D, “*Bromus* with pappus” and “*Bromus* with non-pappus” labels mean that *Bromus* seedlings competed with seedlings reared from the seed morph of *C. solstitialis* with and without a pappus, respectively. Data are means  $\pm$  SE of 13 pots for densities 1 and 2, and five pots for densities 10 and 20. *Centaurea solstitialis*:  $F_{\text{Seed morph}} = 211.961$ ,  $df = 1$  and 758,  $P < 0.001$ ;  $F_{\text{Competition treatment}} = 28.068$ ,  $df = 2$  and 758,  $P < 0.001$ ;  $F_{\text{Density}} = 80.021$ ,  $df = 3$  and 758,  $P < 0.001$ ;  $F_{\text{Seed morph*Competition treatment}} = 2.435$ ,  $df = 2$  and 758,  $P = 0.088$ ;  $F_{\text{Seed morph*Density}} = 15.152$ ,  $df = 3$  and 758,  $P < 0.001$ ;  $F_{\text{Competition treatment*Density}} = 13.825$ ,  $df = 6$  and 758,  $P < 0.001$ ;  $F_{\text{Seed morph*Competition treatment*Density}} = 6.302$ ,  $df = 6$  and 758,  $P < 0.001$ . *Bromus*:  $F_{\text{Seed morph}} = 2.103$ ,  $df = 1$  and 194,  $P = 0.149$ ;  $F_{\text{Density}} = 3.930$ ,  $df = 3$  and 194,  $P = 0.009$ ;  $F_{\text{Seed morph*Density}} = 0.355$ ,  $df = 3$  and 194,  $P = 0.786$ . Asterisks inside panels indicate significant differences between seed morphs at  $P \leq 0.001$ .

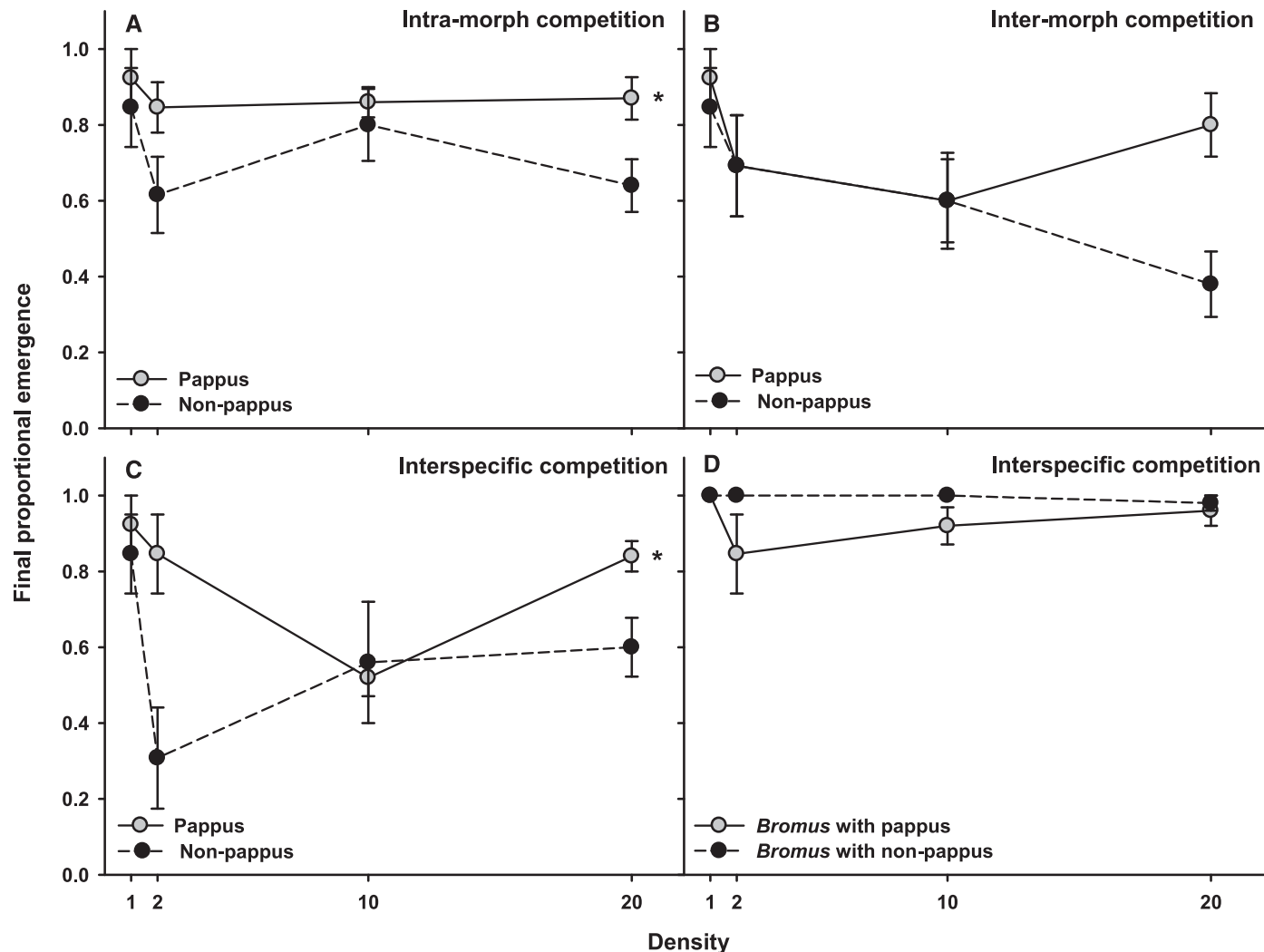
and autumn ( $P = 0.127$ ), and it was much higher in those seasons than in winter ( $P = 0.002$  and  $P < 0.001$ , respectively).

**B. Anemochory**—*Centaurea solstitialis* seeds were found only in seed traps located at 0 m (96% of the total number of collected seeds), 1 m (3%), and 2 m (1%) from source populations ( $F_{\text{Seed morph}} = 6.247$ ,  $df = 1$  and 798,  $P = 0.013$ ;  $F_{\text{Distance}} = 30.237$ ,  $df = 6$  and 798,  $P < 0.001$ ;  $F_{\text{Time}} = 381.301$ ,  $df = 2$  and 798,  $P < 0.001$ ;  $F_{\text{Seed morph*Distance}} = 7.890$ ,  $df = 6$  and 798,  $P < 0.001$ ;  $F_{\text{Seed morph*Time}} = 3.594$ ,  $df = 2$  and 798,  $P = 0.028$ ;  $F_{\text{Distance*Time}} = 5.757$ ,  $df = 12$  and 798,  $P < 0.001$ ;  $F_{\text{Seed morph*Distance*Time}} = 5.071$ ,  $df = 12$  and 798,  $P < 0.001$ ; 0 m vs. the rest,  $P < 0.001$ ; pairwise comparisons between all other distances,  $P > 0.05$ ), and non-pappus seeds were present only at 0 m (Appendix S2). Pappus seeds were statistically more abundant than non-pappus seeds only at the closest

distance from the source population, where the number of pappus seeds was over eight and three times larger than the number of non-pappus seeds in summer and autumn, respectively ( $P < 0.001$  for both cases). The largest number of seeds was recovered from traps in summer and autumn (summer vs. autumn,  $P = 0.437$ ; summer vs. winter,  $P < 0.001$ ; autumn vs. winter,  $P < 0.001$ ).

## DISCUSSION

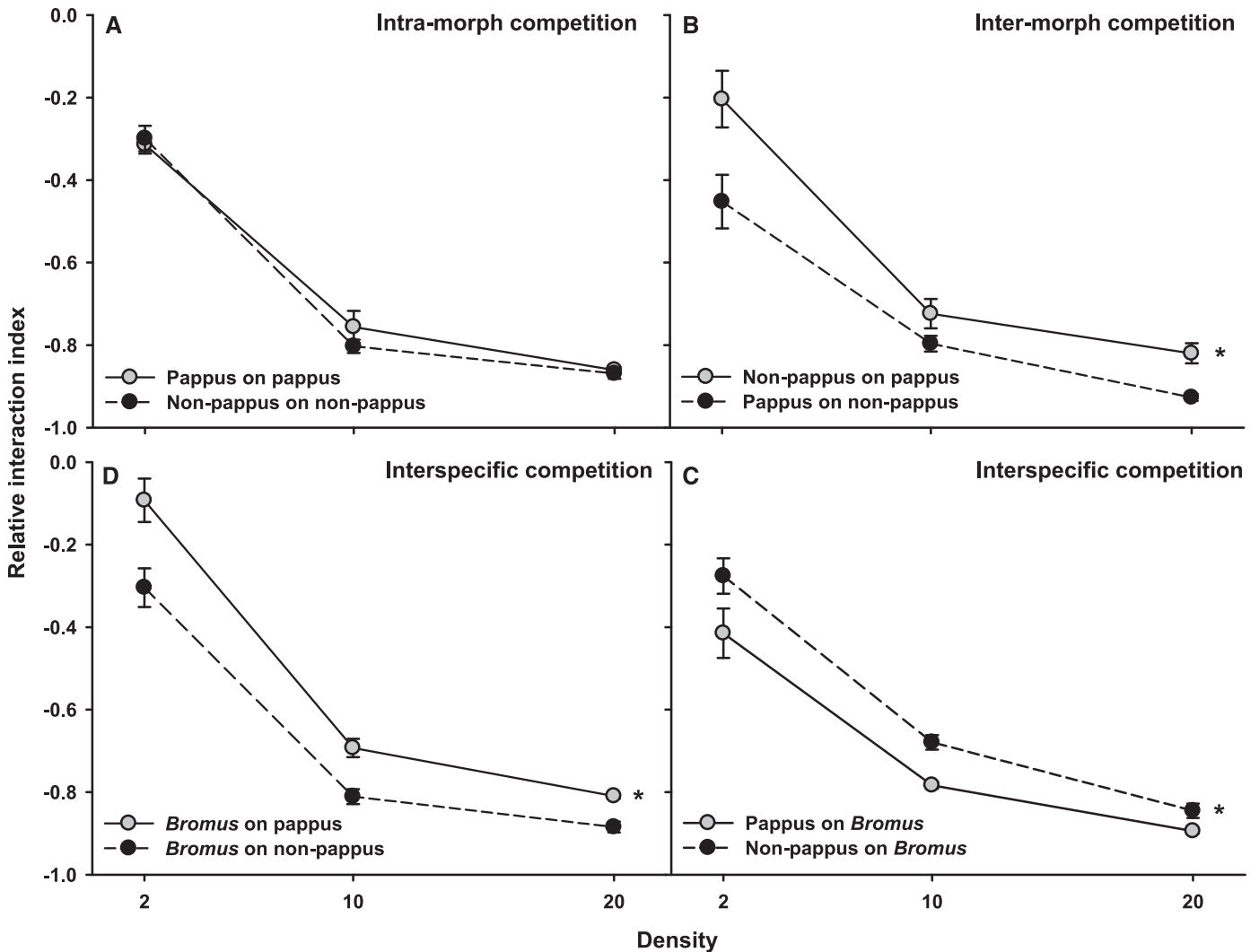
Heterocarpic plants provide suitable models to explore the correlation between functional traits of seed morphs and of the individuals recruited from these morphs; heterocarpy thus has important implications for species survival and reproduction in diverse and



**FIGURE 2** Final proportional emergence of *Centaurea solstitialis* seedlings derived from pappus and non-pappus seeds in the intramorph (A), inter-morph (B), and interspecific competition treatments (C). Seedling emergence of *Bromus catharticus* var. *rupestris* (*Bromus*) (D) is shown for the inter-specific treatment. In D, “*Bromus* with pappus” and “*Bromus* with non-pappus” labels mean that *Bromus* seedlings competed with seedlings reared from the seed morph of *C. solstitialis* with and without a pappus, respectively. Data are means  $\pm$  SE of 13 pots for densities 1 and 2, and five pots for densities 10 and 20. *Centaurea solstitialis*:  $F_{\text{Seed morph}} = 13.534$ ,  $df = 1$  and  $758$ ,  $P < 0.001$ ;  $F_{\text{Competition treatment}} = 2.549$ ,  $df = 2$  and  $758$ ,  $P = 0.079$ ;  $F_{\text{Density}} = 3.606$ ,  $df = 3$  and  $758$ ,  $P = 0.013$ ;  $F_{\text{Seed morph*Competition treatment}} = 0.255$ ,  $df = 2$  and  $758$ ,  $P = 0.775$ ;  $F_{\text{Seed morph*Density}} = 3.989$ ,  $df = 3$  and  $758$ ,  $P = 0.008$ ;  $F_{\text{Competition treatment*Density}} = 1.414$ ,  $df = 6$  and  $758$ ,  $P = 0.206$ ;  $F_{\text{Seed morph*Competition treatment*Density}} = 0.930$ ,  $df = 6$  and  $758$ ,  $P = 0.473$ . *Bromus*:  $F_{\text{Seed morph}} = 0.369$ ,  $df = 1$  and  $194$ ,  $P = 0.544$ ;  $F_{\text{Density}} = 0.349$ ,  $df = 3$  and  $194$ ,  $P = 0.790$ ;  $F_{\text{Seed morph*Density}} = 0.987$ ,  $df = 3$  and  $194$ ,  $P = 0.400$ . Asterisks inside panels indicate significant differences between seed morphs at  $P < 0.05$ .

dynamic environments (Rubio de Casas et al., 2015). Dubois and Cheptou (2012) reported a trade-off between colonization and competition for individuals resulting from the dimorphic seeds of *Crepis sancta*, a species with no seed dormancy, no difference in seed reserves, and increased anemochory of slower-germinating seeds. Similarly, a negative correlation between competition and colonization can be expected within seed morphs of species with enhanced anemochory of smaller seeds (Weiss, 1980; Cheplick and Quinn, 1982; Cheplick and Quinn, 1983; Imbert et al., 1997; Cheplick and Wickstrom, 1999). Here, we explored how colonization and competition are related in the seed morphs of a species with differences in seed size and exozoochory, *C. solstitialis*. We found that seeds with a pappus were larger and displayed increased dispersal abilities compared to those without a pappus, and seedlings

from pappus seeds emerged at faster rates and larger proportions and were better competitors than those from non-pappus seeds. Thus, we observed no evidence for a competition–colonization trade-off for the dimorphic seeds of *C. solstitialis*, offering support to our hypothesis. Our findings then raise the possibility that increased competition does not come at the expense of decreased colonization in seed morphs of heterocarpic species with enhanced exozoochory of larger seeds. In addition, our results suggest that pappus and non-pappus seeds display a task-division strategy in which pappus morphs colonize and preempt unoccupied sites through superior spatial dispersal and fast and large emergence of seedlings with increased competitive abilities, whereas non-pappus seed morphs contribute to persistence at a site through delayed germination and dormancy (i.e., temporal dispersal). This strategy



**FIGURE 3** Relative interaction index (RII) for seedlings emerging from pappus and non-pappus seeds of *Centaurea solstitialis* growing together under intramorph (A), intermorph (B), and interspecific treatments (C). For the interspecific treatment, indices based on the biomass of *Bromus catharticus* var. *rupestris* (*Bromus*) are also shown (D). In C, “*Bromus* on pappus” and “*Bromus* on non-pappus” labels mean that symbols show the competitive effects of *Bromus* seedlings on those from *C. solstitialis* pappus and non-pappus seeds, respectively. Similarly, in D, “Pappus on *Bromus*” and “Non-pappus on *Bromus*” labels mean that symbols show the competitive effects of seedlings from pappus and non-pappus seeds of *C. solstitialis*, respectively, on *Bromus* seedlings. Data are means  $\pm$  SD of 13 seedlings for density 1 and density 2 in the intermorph and interspecific treatments, whereas they are grand means  $\pm$  SD of the mean RII per plot of 13 pots for density 2 in the intramorphic treatment and five pots for densities 10 and 20 in the intramorphic, intermorph, and interspecific treatments. *Centaurea solstitialis*:  $F_{\text{Seed morph}} = 51.624$ ,  $df = 1$  and  $684$ ,  $P < 0.001$ ;  $F_{\text{Competition treatment}} = 6.270$ ,  $df = 2$  and  $684$ ,  $P = 0.002$ ;  $F_{\text{Density}} = 588.561$ ,  $df = 2$  and  $684$ ,  $P < 0.001$ ;  $F_{\text{Seed morph*Competition treatment}} = 11.954$ ,  $df = 6$  and  $684$ ,  $P < 0.001$ ;  $F_{\text{Seed morph*Density}} = 3.130$ ,  $df = 2$  and  $684$ ,  $P = 0.044$ ;  $F_{\text{Competition treatment*Density}} = 2.010$ ,  $df = 4$  and  $684$ ,  $P = 0.091$ ;  $F_{\text{Seed morph*Competition treatment*Density}} = 2.359$ ,  $df = 4$  and  $684$ ,  $P = 0.052$ . *Bromus*:  $F_{\text{Seed morph}} = 35.183$ ,  $df = 1$  and  $170$ ,  $P < 0.001$ ;  $F_{\text{Density}} = 322.413$ ,  $df = 2$  and  $170$ ,  $P < 0.001$ ;  $F_{\text{Seed morph*Density}} = 3.017$ ,  $df = 2$  and  $170$ ,  $P = 0.052$ . Asterisks inside panels indicate significant differences between seed morphs at  $P < 0.001$ .

may have profound consequences for the fitness of the species in environments with high variation in both space and time (Venable and Lawlor, 1980; Venable, 1985b; Snyder, 2006; Buoro and Carlson, 2014), such as central Argentina (Hiero et al., 2009; Chiufo, 2016).

Seedlings from pappus seeds displayed increased competitive abilities compared to those from non-pappus seeds, both when growing with non-pappus seedlings and when growing with *Bromus* seedlings. Both greater mass (Rees and Westoby, 1997) and faster germination (Donohue et al., 2010; Gioria and Pysek, 2017)

in pappus seeds compared to non-pappus seeds could explain these results (Venable, 1985a). We found that larger seeds were richer in endosperm reserves, which may result in stronger seedling competitive ability compared to plants from smaller seeds (Weiss, 1980; Cheplick and Quinn, 1983; Venable, 1985a; Imbert et al., 1997; Cheplick and Wickstrom, 1999; Buckley et al., 2003). Other studies of *C. solstitialis* populations similarly report that bigger seeds produce stronger competitors than populations with smaller seeds (Graebner et al., 2012). Also, early emergence could have provided pappus seedlings a competitive advantage over non-pappus seedlings,

**TABLE 2.** Final aboveground biomass of *Centaurea solstitialis* and *Bromus catharticus* var. *rupestris* (*Bromus*) seedlings in the different treatments of the competition experiment. Data are means  $\pm$  SD of 13 seedlings for density 1 and density 2 in the intermorphic and interspecific treatments, whereas they are grand means  $\pm$  SD of the mean biomass per plot of 13 pots for density 2 in the intramorphic treatment and five pots for densities 10 and 20 in the intramorphic, intermorphic, and interspecific treatments.

Competition treatment	Seed type	Species	Density	Biomass (g)
Seedling growing alone	Pappus	<i>C. solstitialis</i>	1	1.485 $\pm$ 0.357
Seedling growing alone	Non-pappus	<i>C. solstitialis</i>	1	1.890 $\pm$ 0.223
Seedling growing alone	–	<i>Bromus</i>	1	1.925 $\pm$ 0.247
Intramorphic	Pappus	<i>C. solstitialis</i>	2	0.848 $\pm$ 0.193
Intramorphic	Non-pappus	<i>C. solstitialis</i>	2	1.129 $\pm$ 0.279
Intramorphic	Pappus	<i>C. solstitialis</i>	10	0.221 $\pm$ 0.084
Intramorphic	Non-pappus	<i>C. solstitialis</i>	10	0.222 $\pm$ 0.049
Intramorphic	Pappus	<i>C. solstitialis</i>	20	0.116 $\pm$ 0.017
Intramorphic	Non-pappus	<i>C. solstitialis</i>	20	0.141 $\pm$ 0.034
Intermorphic	Pappus	<i>C. solstitialis</i>	2	1.078 $\pm$ 0.518
Intermorphic	Non-pappus	<i>C. solstitialis</i>	2	0.782 $\pm$ 0.467
Intermorphic	Pappus	<i>C. solstitialis</i>	10	0.264 $\pm$ 0.095
Intermorphic	Non-pappus	<i>C. solstitialis</i>	10	0.230 $\pm$ 0.063
Intermorphic	Pappus	<i>C. solstitialis</i>	20	0.154 $\pm$ 0.051
Intermorphic	Non-pappus	<i>C. solstitialis</i>	20	0.075 $\pm$ 0.021
Interspecific	Pappus	<i>C. solstitialis</i>	2	1.311 $\pm$ 0.490
Interspecific	Non-pappus	<i>C. solstitialis</i>	2	1.054 $\pm$ 0.385
Interspecific	Pappus	<i>C. solstitialis</i>	10	0.306 $\pm$ 0.070
Interspecific	Non-pappus	<i>C. solstitialis</i>	10	0.218 $\pm$ 0.059
Interspecific	Pappus	<i>C. solstitialis</i>	20	0.162 $\pm$ 0.013
Interspecific	Non-pappus	<i>C. solstitialis</i>	20	0.119 $\pm$ 0.032
Interspecific	Pappus	<i>Bromus</i>	2	0.860 $\pm$ 0.459
Interspecific	Non-pappus	<i>Bromus</i>	2	1.136 $\pm$ 0.400
Interspecific	Pappus	<i>Bromus</i>	10	0.238 $\pm$ 0.022
Interspecific	Non-pappus	<i>Bromus</i>	10	0.375 $\pm$ 0.056
Interspecific	Pappus	<i>Bromus</i>	20	0.109 $\pm$ 0.014
Interspecific	Non-pappus	<i>Bromus</i>	20	0.164 $\pm$ 0.044

as shown in *Crepis sancta* (Dubois and Cheptou, 2012) and *Heterotheca latifolia* (Venable, 1985a). Because we added pregerminated seeds to pots with seedlings that had not emerged for 10 d to maintain desired seedling densities, our competition estimates are likely to be conservative. Differences in germination between dimorphic seeds, and their ecological consequences for site preemption and persistence, have been shown for a number of species inhabiting unpredictable environments (Venable and Levin, 1985b; Venable et al., 1995; Imbert, 2002), such as central Argentina (Hierro et al., 2009), and are interpreted as a bet-hedging strategy (Venable, 1985b; Philippi, 1993; Clausen and Venable, 2000; Venable, 2007). Our study suggests that in addition to preemption of sites through fast and high proportional germination, colonizing seeds accomplish that task through the increased competitive ability of their seedlings. Seed-coat thickness for pappus and non-pappus morphs showed no differences, and we do not know what triggers different germination velocities and proportions for dimorphic seeds of *C. solstitialis*. Similarly, more work is needed to assess the relative contributions of seed size and germination rate to the competitive abilities of the seedlings derived from the dimorphic seeds of the species.

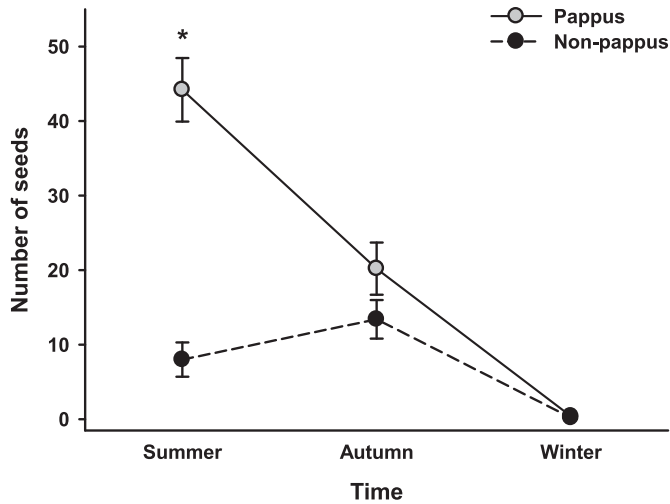
Most seeds fell in close proximity to source populations in our assessment of anemochory, confirming that wind is a poor disperser of *C. solstitialis* seeds (Roché, 1992). Exozoochory, in contrast, might be a major vehicle for seed dispersal. Greater exozoochory in pappus seeds than in non-pappus seeds is in line with the expected importance of the pappus for this dispersal mode. Seed mass is expected to play a key role in anemochory (Cheplick and Quinn,

1982; McEvoy, 1984; Venable and Levin, 1985a; Cheplick and Wickstrom, 1999; Imbert, 2002), whereas permanent dispersal structures are likely to be central in exozoochory (Baskin and Baskin, 2014). The consequences of seed size for competition and anemochory may lead to a general negative correlation between competition and colonization within species with heteromorphic seeds (Weiss, 1980; Cheplick and Quinn, 1983; Imbert et al., 1997; Cheplick and Wickstrom, 1999). Enhanced anemochory is, however, accomplished by the seed morph that produces seedlings with increased competitive abilities in *H. latifolia* (Venable, 1985a), a species with no differences in seed mass, but with larger embryo mass in the seed morphs with superior anemochory (Venable and Levin, 1985a). We also found a positive correlation between competition and colonization, but our study introduces an interesting example in which a permanent dispersal structure, the pappus, confers greater exozoochory to seeds that are heavier and produce stronger competitors than seeds lacking the pappus. The proportion of pappus to non-pappus morphs produced by the capitula in our study (5.439) is similar to that reported for populations in California (Benefield et al., 2001). Thus, *C. solstitialis* appears to devote much more seed allocation to spatial than to temporal dispersal (Buoro and Carlson, 2014; Rubio de Casas et al., 2015). The adaptive nature of differences in seed allocation remains to be addressed.

Consistent with our findings, previous experiments conducted with *C. solstitialis* populations collected from much of the native and nonnative range of the species detected differences in germination rates and proportions between pappus and non-pappus seeds for Argentinean populations (Hierro et al., 2009). Differences between seed morphs were, however, not found in the rest of the study populations. Metrics of environmental risk, such as the coefficient of variation in winter precipitation, were also larger in central Argentina than in the rest of the regions included in the study and correlated well with germination responses of *C. solstitialis* populations (Hierro et al., 2009). Thus, our results may be influenced by the very recent evolutionary history of the species in central Argentina (Eriksen et al., 2014; Barker et al., 2017), including adaptation to exceptionally variable environments (Venable, 2007; Hierro et al., 2009, 2013; Gremer et al., 2016). Functional roles of dimorphic seeds within organisms may not be fixed, but rather may vary in response to local environmental conditions.

Our results confirm that dispersal in space and time is negatively associated in seed morphs of Argentinean populations of *C. solstitialis* (Hierro et al., 2009), as predicted by theory (Venable and Lawlor, 1980; Buoro and Carlson, 2014; Rubio de Casas et al., 2015) and found in other species with seed dimorphism (Venable and Lawlor, 1980; McEvoy, 1984; Venable and Levin, 1985a; Imbert, 1999). Providing empirical evidence for that trade-off has recently been singled out, however, as a priority for the dispersal research





**FIGURE 4** Numbers of pappus and non-pappus seeds collected from peltis of three common mammal species in the study area throughout the seed-dispersal time of *Centaurea solstitialis* (i.e., exozoochory). Data have been corrected to comply with the departure from a 1:1 proportion in the number of seed morphs in capitula (see text). Data are means  $\pm$  SE of five populations. Asterisks indicate significant differences between seed morphs at  $P < 0.001$ .

agenda (Buoro and Carlson, 2014). This trade-off is also thought to be adaptive under unpredictable environmental conditions and to have major consequences for site colonization and persistence (Buoro and Carlson, 2014). In addition, theory predicts that environments varying in both spatial and temporal conditions (i.e., negative and weak autocorrelation) select for dispersal through both space and time (Snyder, 2006; Buoro and Carlson, 2014). The Caldenal exhibits not only large temporal variation (Hierro et al., 2009), but also considerable spatial variation generated by the frequent and widespread occurrence of disturbance, including soil turnover by fossorial animals, grazing by native and nonnative herbivores, fire, plowing, and road construction and maintenance (Chiuffo, 2016). Pappus seeds with increased dispersal and germination (i.e., decreased dormancy) and non-pappus seeds with decreased dispersal and delayed germination may allow *C. solstitialis* to successfully exploit both sources of variation. The presence of a dispersal-dormancy trade-off and the lack of a competition-colonization trade-off within *C. solstitialis* seed morphs likely contribute to the high relative abundance and wide distribution of the species in the Caldenal of central Argentina (Hierro et al., 2006, 2013, 2017). Future studies should address the extent of heterocarpy and the nature of correlations between ecological functions of seeds in the herbaceous community (Siewert and Tielbörger, 2010) of the Caldenal, including both native and nonnative members.

Differences in the ecological functions performed by the dimorphic seeds of species can be part of the classical adaptive dilemmas faced by organisms (Harper, 1977; Venable, 1985b; Imbert, 2002; Dubois and Cheptou, 2012; Grime and Pierce, 2012). Consequently, task division between dimorphic seeds may allow species to overcome limitations imposed by trade-offs. Consistent with this idea, variation in dispersal, germination, and competition reported here suggest that pappus and non-pappus seeds help *C. solstitialis* to accomplish mutually exclusive functional roles and, thus, cope with highly variable environments.

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