Eco-evolutionary causes and consequences of rarity in plants: a meta-analysis

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Summary

- Species differ dramatically in their prevalence in the natural world, with many species characterized as rare due to restricted geographic distribution, low local abundance and/or habitat specialization.
- We investigated the ecoevolutionary causes and consequences of rarity with phylogenetically controlled metaanalyses of population genetic diversity, fitness and functional traits in rare and common congeneric plant species. Our syntheses included 252 rare species and 267 common congeners reported in 153 peer-reviewed articles published from 1978 to 2020 and one manuscript in press.
- Rare species have reduced population genetic diversity, depressed fitness and smaller reproductive structures than common congeners. Rare species also could suffer from inbreeding depression and reduced fertilization efficiency.
- By limiting their capacity to adapt and migrate, these characteristics could influence contemporary patterns of rarity and increase the susceptibility of rare species to rapid environmental change. We recommend that future studies present more nuanced data on the extent of rarity in focal species, expose rare and common species to ecologically relevant treatments, including reciprocal transplants, and conduct quantitative genetic and population genomic analyses across a greater array of systems. This research could elucidate the processes that contribute to rarity and generate robust predictions of extinction risks under global change.

Introduction

In the natural world, species differ drastically in their prevalence (Stebbins, 1942; Preston, 1948; MacArthur, 1957; Rabinowitz *et al*., 1986; Darwin, 1988; May, 1999; Murray *et al*., 2002; McGill *et al*., 2007), but the biological factors that influence such patterns are not well understood. Rare species are generally characterized by restricted geographic distribution, low local abundance and/or narrow habitat specialization (Rabinowitz, 1981). More than one-third of land plant species are rare or very rare (Enquist *et al*., 2019). As a broad taxonomic group, plants show historically persistent patterns of rarity and commonness independent of modern anthropogenic influences (Stein *et al*., 2000; Domínguez Lozano & Schwartz, 2005; Enquist *et al*., 2019). Despite their limited representation in communities, rare species play various important roles in ecosystem functions, such as nutrient cycling (Theodose *et al*., 1996), trophic dynamics (Bracken & Low, 2012) and resistance to biological invasions (Lyons & Schwartz, 2001). Rare species can also act as indicators of biodiversity (Zavaleta & Hulvey, 2004), and guide conservation priorities (Lawler *et al*., 2003). Investigating the ecological and evolutionary causes and consequences of rarity could advance ecological theory and guide conservation efforts (Bevill & Louda, 1999), especially in the context of rapid global change (Van Calster *et al*., 2008; Mouillot *et al*., 2013).

Functional traits strongly affect species performance (Kunin & Gaston, 1997; Albert *et al*., 2011) and coexistence (Kraft *et al*., 2015). Studies contrasting rare and common congeneric species could illuminate the ecoevolutionary factors that contribute to rarity (Combs *et al*., 2013) by controlling for the effects of life history and phylogeny (Kunin & Gaston, 1997; Godt & Hamrick, 2001; Murray *et al*., 2002; Farnsworth, 2007). Murray *et al*. (2002) reviewed *c*. 50 comparative studies that collectively examined a wide range of traits and fitness components in congeneric rare vs common species published before 2002; while most studies investigated different traits, those that measured similar traits often generated mixed results. Bevill & Louda (1999) reviewed *c*. 40 studies comparing the demography of rare and common species, and concluded that studies were inconsistent in the traits measured. Overall, comparisons of fitness and/or functional traits

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of rare and common species have been relatively infrequent, and those that exist tend to be autoecological in nature and inconclusive (Bevill & Louda, 1999; Munzbergova, 2005; Combs *et al.*, 2013). Some empirical studies have found that rare endemic species are shorter in stature, produce fewer but larger seeds and are less likely to reproduce vegetatively than common species (Lavergne *et al.*, 2004; Farnsworth, 2007), all of which could impede their ability to disperse and establish in new locations. Additionally, rare species could exhibit low phenotypic plasticity (Murray *et al.*, 2002), which could restrict range expansions across variable environments and acclimation *in situ* to global change (Nicotra *et al.*, 2010). However, the degree of adaptive plasticity expressed by a rare species will depend on the extent of spatial and temporal heterogeneity in conditions, and rare species from more variable habitats can exhibit greater plasticity than their common congeners (Boyd *et al.*, 2022). To date, few studies have examined plasticity in the context of rarity (Liao *et al.*, 2006; Lovell & McKay, 2015; Rutherford *et al.*, 2017).

The capacity of species to adapt to environmental change depends on their genetic diversity (Frankham, 2005; Futuyma, 2010), but theory suggests that rare species suffer from low genetic variability due to the effects of genetic drift (Wright, 1931) and persistent directional natural selection in rare habitats (Van Valen, 1965). Indeed, rare species often exhibit reduced population genetic variation (Karron, 1987; Gitzendanner & Soltis, 2000; Cole, 2003). However, genetic differences between rare and common species can be minimal. For example, *Daviesia suaveolens* (Fabaceae) is a rare shrub with a restricted geographic range, but large population sizes within that range; this rare species had similar levels of genetic variation as its widespread and common congener, *Daviesia mimosoides* (Young & Brown, 1996).

Ultimately, comparisons of genetic diversity, fitness and functional traits of rare and more common congeneric species could provide insight into species rarity especially within the context of environmental change. Yet, this broad body of such research has not been comprehensively reviewed in nearly two decades and has not yet been synthesized with metaanalytic techniques. Furthermore, the extent of rarity could influence ecological and evolutionary outcomes. Rabinowitz (1981) proposed seven types of rarity that exist across three axes: geographic distribution (widespread vs restricted), local abundance (locally common vs sparse), and habitat specificity (generalist or specialist to a frequent habitat type vs specialist to a rare habitat). Variation along these axes results in eight different categories of species, one of which Rabinowitz (1981) defined as common (widespread, locally common, generalist) and seven of which can be classified as rare. Species that exist along multiple dimensions of rarity could display more severe reductions in genetic diversity and fitness relative to their common congeners, and could be more vulnerable to global change than species categorized as rare along only one axis. To examine if rarity is associated with reduced genetic variation, lower fitness and differences in functional traits (Table 1), we conducted a series of comprehensive phylogenetically controlled metaanalyses of comparative congeneric studies of plants from the past four decades, and we discuss these results in the context of the seven types of rarity originally proposed by Rabinowitz (1981).

Materials and Methods

Literature search, eligibility criteria and datasets

We searched *ISI Web of Science* (Thompson Reuters, New York, NY, USA) in January 2021 to screen the primary literature for studies published before 2021 that compared population genetic diversity, fitness and functional traits of rare and common congeneric plant species. We used the syntax *TS= (((rare AND (common OR widespread OR dominant*)) OR rarity) AND species AND plant*)* in the advanced search tool to return a list of 4096 articles. We filtered this list by article type to exclude reviews, proceedings papers, editorial material, book chapters, corrections, notes, letters, data papers and news items, which resulted in 3777 articles. We defined strict eligibility criteria for inclusion in our metaanalysis, which we describe in depth in the Supporting Information Methods S1 along with details about data extraction. This initial literature review identified 330 studies from

Table 1 Hypotheses, predictions and results for our metaanalysis comparing rare plant species with their common congeners.

Hypothesis	Prediction	Metaanalysis results
Rare species have restricted genetic variation	Reduced population genetic variation and more inbreeding (lower F_{IS})	Confirmed for genetic diversity parameters, but no signal of rarity for F_{IS} (Fig. 1)
Rare species have reduced fitness	Lower juvenile recruitment, survival, growth and fecundity	Confirmed for survival and later components of fitness (Fig. 2)
Rare species differ in functional traits	Smaller size of vegetative and reproductive organs, reduced physiological performance, delayed phenology, increased damage from natural enemies, reduced interactions with mutualists such as pollinators, reduced plasticity	Smaller reproductive organs, but no additional signature of rarity in functional traits (Fig. 2)
Rare species have less efficient pollination syndromes and are limited by mating opportunities	Less efficient pollination, reduced rates of outcrossing in field studies	Preliminary mating system metaanalysis shows that rare species could have less efficient pollination (reduced fitness under hand-pollination and self-pollination; Fig. 3). Additional research is required to test for pollinator limitation

1978 to 2020 that could yield species-level fitness measures, functional trait values and/or population genetic diversity parameters of rare and common plant congeners. In all cases, the authors of the original studies classified the focal species as rare vs common. Importantly, we included only studies in which the data for both the common and the rare species were reported; to control for methodological differences, we did not compare common and rare congeners across studies. We eliminated studies using nonnative species because their occurrence does not reflect entirely natural processes. We screened the full text of these studies for relevant data, retaining 153 studies (Table S1). For rare and common species, we extracted means, standard deviations and sample sizes for neutral genetic parameters, continuous functional trait values and fitness components, and the numbers of events and sample sizes for binary fitness measures (e.g. germination success).

For each rare species in each study, we categorized the type of rarity along Rabinowitz's (1981) three primary axes: geographic distribution, habitat specialization and local abundance. All studies included in our metaanalysis referenced these rarity dimensions directly and/or described the rare species in ways that allowed us to classify rarity along these dimensions. Specifically, rare species were categorized as having narrow geographic distribution if their range was described as smaller than that of more widespread common species. Rare species were categorized as having low local abundance if the numbers of individuals, percentage cover or frequency of occurrence in a defined location were described as less than that of more abundant common species. Lastly, rare species were categorized as habitat specialists if their habitat association was described as limited and in more restrictive terms than the habitat(s) in which more generalist common species occurred. Some studies described species rarity across multiple dimensions. For example, *Pityopsis ruthii* was described as 'endemic' given its narrow geographic distribution and habitat specialization to exposed boulders along just two rivers in Tennessee (Boyd *et al.*, 2022); we categorized this species along both of these axes of rarity for our analyses. In cases in which multiple studies of a single rare species described rarity differently, we elected to use the most restrictive description. Most rare species in our datasets were described as geographically restricted.

Population genetic dataset We retained 31 studies that evaluated population genetic parameters in natural populations of rare and widespread congeners (Table S2). Most studies quantified genetic diversity through the number of alleles per locus (27 studies), the percentage of loci that were polymorphic (22 studies), and observed and expected heterozygosity (22 studies for both). Only 10 studies reported F_{IS} (the inbreeding coefficient) and seven studies reported F_{ST} (the fixation index). This dataset includes 37 rare and 37 common species or subspecies from 31 genera and 20 families; the retained studies sampled an average of 6.64 (±3.8 SD, range: 2–15) natural populations of rare species and an average of 8.67 (±7.5 SD, range: 2–43) populations of the common congener. All but eight of the studies focused on a single pair of rare–common congeners species. Most studies used allozymes (21 studies), with fewer studies relying on microsatellite (six studies), random amplification of polymorphic DNA (RAPD; one study) or intersimple sequence repeat (ISSR) markers (three studies). Only two rare and four common species had a primarily self-fertilizing mating system; the remaining species were either obligate outcrossers or had mixed mating systems. Most species in the dataset were perennials, with only four rare and six common species having annual life history strategies.

Fitness and functional traits We extracted data from 73 studies reporting binary components of fitness (i.e. recruitment, survival, reproductive success and damage from natural enemies; Table S3). This dataset includes 131 rare and 132 common species or subspecies representing 88 genera from 45 families. Approximately two-thirds of the studies focused on a single rare species, which was contrasted with one or more common congeners. Additionally, we retained 99 studies for data extraction reporting continuous measures of functional traits and fitness components (fecundity, growth, demographic transitions and vegetative reproduction; Table S3). The studies that we included in this analysis can be classified into five categories: observational studies of natural populations in the field; laboratory experiments under controlled conditions using accessions collected from natural populations; ecological experiments in natural field settings, manipulating abiotic or biotic factors and measuring naturally occurring focal individuals; common garden or reciprocal transplant experiments in the field using transplanted accessions; and a combination of the last two approaches (ecological manipulations in common garden or transplant experiments in the field; Table S4).

We classified metrics associated with flower and seed production, vegetative reproduction and male fitness as fitness. We also categorized seed size as a fitness component because it can influence germination and seedling establishment success (Moles & Westoby, 2004). Many studies reported multiple components of fitness (e.g. number of inflorescences, number of flowers per inflorescence and seed set per flower) along with composite fitness values (e.g. total seed set). In those cases, we extracted data from the variable that most closely reflected lifetime fitness (e.g. seeds per plant). We also extracted data on functional traits that are often subject to strong selection and could influence plant responses to rapid environmental change, including plant size, biomass allocation, physiology, phenology, plasticity, size of reproductive structures, and interactions with mutualists (i.e. pollinator visitation rates, mycorrhizal associations) and antagonists (i.e. herbivores; Table S3). The size of reproductive structures included floral organ size and fruit dimensions, as pollinators typically prefer larger flowers (Krizek & Anderson, 2013), thereby augmenting outcrossing rates, and fruit size can influence dispersal dynamics (Correa *et al.*, 2018; Valenta & Nevo, 2020). This dataset includes 163 rare and 178 common species from 108 genera and 49 families. As with our binary dataset, most species were the focus of a single study, and approximately two-thirds of the studies focused on a single rare species. Only *c.* 40% of studies in either dataset manipulated the abiotic or biotic environment (e.g. light, temperature, water, pollination, competition and herbivory) with some studies including multiple factors.

Data analyses

We conducted phylogenetically corrected multilevel mixed effect metaanalyses using the R package METAFOR (v.2.1-0; Viechtbauer, 2010), with random effects for publication identity, effect size within publication, nonphylogenetic species effects and phylogeny to account for nonindependence of multiple measurements from the same study and phylogenetic relatedness. By including a random effect for nonphylogenetic species effects, we accounted for evolutionary history and similarities due to ecological factors and life histories (Hadfield & Nakagawa, 2010; Cinar *et al.*, 2022). Additionally, we accounted for phylogenetic similarity across genera by including a phylogenetic correlation matrix as a random effect in all metaanalyses. These steps reduced the risk of spurious results from shared ancestry (Lajeunesse, 2009). To reconstruct these phylogenies, we used the Open Tree of Life (ROTL package; Hinchliff *et al.*, 2015; Michonneau *et al.*, 2016), the *compute.brlen* function of the APE package (Paradis & Schliep, 2019) to calculate branch lengths and the *vcv.phylo* function of the APE package to calculate the phylogenetic correlation matrix. We did not include moderators for publication year, latitude, longitude or elevation, as preliminary analyses of all datasets indicated that these covariates were nonsignificant.

For continuous data, we calculated the standardized mean difference (Hedge's *g*) as the effect size through contrasting various parameters (i.e. genetic diversity, functional traits or fitness components) of rare and common congeners measured in the same study. For the dataset on binary components of fitness, we used the log of the odds ratio as the effect size. We computed effect sizes such that values of Hedge's *g* or log of the odds ratio < 0 indicated that the rare species had lower trait, fitness or genetic diversity values relative to the common species. To include binary and continuous metrics of fitness and functional traits within the same metaanalysis, we converted the log odds ratio effect sizes for binary variables to Hedge's *g* using the R package COMPUTE.ES (Del Re, 2013), based on previously developed computations (Chinn, 2000). Combined, the continuous and binary datasets included 124 studies, which quantified fitness components and functional traits in 223 rare species and 236 common species from 141 genera and 57 families (Table S3).

Some studies included more than one rare or common species of the same genus; for example, Lovell & McKay (2015) compared neutral and quantitative genetic diversity of two common vs two rare species of *Boechera* (Brassicaceae). In those cases, we used the R package DMETAR (v.0.0.9; Harrer *et al.*, 2019) to aggregate means, standard deviations and sample sizes within studies across species to create one set of values for the common species (e.g. common *Boechera*) to contrast against one set for the rare species (e.g. rare *Boechera*). In the trait and fecundity dataset, we also used this procedure to pool across separate populations, sites or other grouping factors (e.g. replicates or developmental stages). For binary data, we aggregated data within a study by summing the numbers of events and sample sizes. In some cases, studies reported correlated traits (e.g. biomass, height, number of leaves); thus, we calculated weighted mean effect sizes across these traits through preliminary within-study fixed-effect metaanalyses (the two-step method recommended by Song *et al.*, 2020), which we grouped into one larger category (e.g. size) to avoid pseudoreplication.

For the 40% of studies that quantified fitness or trait differences between rare and common congeneric species in response to experimental treatments, we aggregated effect sizes across treatment levels using the R package DMETAR (v.0.0.9) (Harrer *et al.*, 2019) when the ecological relevance of treatment levels was not clear (e.g. different sites without clear environmental differences, living samples vs herbarium samples, herbicide types but not concentrations, etc.). When treatment levels were ecologically relevant, we did not aggregate effect sizes within a study. However, manipulations and treatment levels were idiosyncratic, with very few similarities across studies, leading to a dataset with > 90 types of experiments (e.g. abscisic acid application, soil nutrient amendment, drought vs waterlogging, competition manipulations). To enable synthesis of studies that applied very different conditions, we characterized treatments as varying in abiotic (light, nutrient, temperature, water or fire) or biotic (pollination, competition, herbivory, belowground associates) factors. If there were more than three levels of an environmental treatment in a study, treatment levels were condensed to three by pooling effect sizes to represent low, intermediate and high treatment levels. We recorded if each study was conducted in a field, glasshouse, growth chamber or other setting.

Population genetics We tested the hypotheses that rare species have reduced genetic diversity, greater levels of neutral population genetic divergence and increased inbreeding. A preliminary analysis revealed no significant effect of life history stage or breeding system on effect sizes; thus, we excluded these terms from the model. The final phylogenetic multilevel metaanalysis model included a moderating factor for neutral genetic parameters (i.e. percentage polymorphism, number of alleles per locus, observed and expected heterozygosity, F_{IS} and F_{ST}), as well as all four random effects described above (publication identity, effect size, nonphylogenetic species effect and phylogeny).

Fitness components and functional traits We used the binary and continuous datasets to test the hypothesis that rare species express different trait values and have reduced fitness than common congeners. To do so, our multilevel phylogenetically corrected mixed effect metaanalysis contrasted rare and common species for the aforementioned functional traits and fitness components, and included all four random effects (publication identity, effect size, nonphylogenetic species effect and phylogeny). We explored the effect of various moderators on this contrast, including rarity type, fitness or trait category, and environment. The final model included a moderator for the fitness/trait category because preliminary models found no significant effects of other moderators. The dataset did not have sufficient replication across studies to examine synergistic effects of fitness/trait type with other variables such as rarity type or environment. We excluded data from treatments in which the mating system was manipulated (see below), but included studies that recorded fitness under other treatments.

Pollination manipulations We hypothesize that rare species could be limited by mating opportunities, which could favor the evolution of self-compatibility. To test this hypothesis, we examined reproductive fitness in the subset of studies that manipulated pollination through selfing (via emasculation and application of selfed pollen to the stigma), supplemental pollination (additional pollen provided to open-pollinated flowers) or hand pollination (emasculation and application of pollen from a distinct individual or pool of individuals of the same species). For studies that conducted these manipulations, we also retained open pollination treatments as unmanipulated controls. If rare species are more pollen-limited than common species, they would show greater fitness under supplemental pollination than would their common congeners. If rare species have greater rates of self-compatibility, they would have higher fitness than their common congeners under selfing. Finally, if fertilization after pollen deposition is less efficient in rare than in common species, we expect rare species to be at a fitness disadvantage under hand pollination. Species in this metaanalysis either had a mixed-mating or obligate outcrossing breeding system; only three rare species differed in mating system from their common congener (Table S3). Only $n = 14$ studies manipulated mating system dynamics in a total of 25 rare and 25 common species from 15 genera and 12 families (Table S3).

Publication bias diagnostics To assess publication bias, we computed the fail-safe number for each metaanalysis using Rosenthal's (1979) method. The fail-safe number estimates the number of additional nonsignificant studies that would have to be added to the dataset to make the metaanalysis results nonsignificant. When the fail-safe number is large compared with the sample size, results of metaanalysis are considered to reflect the true effect, and indicate that the metaanalysis is robust to publication bias. We also calculated the ratio of the fail-safe number to Rosenthal's critical value ($\geq 5n + 10$, where n = sample size of studies), with ratios > 1 exceeding Rosenthal's (1979) criterion. The fail-safe number does not account for random effects, and should, therefore, be interpreted cautiously. Second, we visualized potential publication bias through funnel plots of standard error vs effect size. If publication bias exists against small studies showing no statistical difference between rare and common species, these funnel plots would show asymmetry toward studies with higher standard errors (near the base of the funnel).

Results

Population genetic dataset

We detected a significant effect of population genetic parameter type on the comparison of rare and common species ($QM = 28.3$, $df = 6$, $P < 0.0001$; Table S5). As predicted, rare species have significantly lower genetic diversity than common species, measured as the percentage of loci that are polymorphic, the number of alleles per locus, and expected and observed heterozygosity (Fig. 1). We detected no signature of rarity on population genetic differentiation (F_{ST}) or the inbreeding coefficient (F_{IS}), yet few studies reported these parameters, and the fail-safe numbers for these parameters were quite low (fail-safe numbers: $F_{IS} = 14$; $F_{ST} = 0$; Table S5; Fig. 1). The overall fail-safe number (5050, $P < 0.0001$) was high, as were the fail-safe numbers for all genetic diversity parameters (Fig. 1; Table S5), suggesting limited publication bias. This dataset had 31 total studies, leading to a fail-safe ratio (fail-safe number divided by $5n + 10$, where n = sample size of studies) of 30.6, which is greater than the value of 1 needed to pass Rosenthal's test (Rosenthal, 1979). However, the funnel plot (Fig. S1) was not symmetrical ($z = -7.85$, $P < 0.0001$), indicating that more studies are needed to evaluate the degree to which rarity reduces genetic diversity. Furthermore, limited sample sizes prevented us from evaluating the effects of rarity type, life history or other ecological factors on population genetic parameters.

Fitness components and functional traits

We detected a significant main effect of fitness/trait type ($QM = 31.5$, $df = 14$, $P = 0.0048$), with rare species showing lower survival and fitness, along with smaller reproductive structures than their common congeners (Fig. 2; Table S6). However, we found no differences in functional traits across rare and common congeners. The overall fail-safe number was high (fail-safe $n = 3609$, $P < 0.0001$), suggesting limited publication bias. With 125 studies in the dataset, the fail-safe ratio of 5.7 exceeds the value of 1 needed to pass Rosenthal's (1979) test. The funnel plot does not appear to be asymmetrical ($z = -0.61$, $P = 0.54$, Fig. S2). Nevertheless, the low fail-safe numbers and limited sample sizes for some trait/fitness categories indicate that additional studies are needed (Table S6). For example, the fail-safe number was 0 for survival, suggesting that additional studies are warranted. Similarly, low fail-safe numbers for growth rates, biomass allocation to shoots and to leaves, and interactions with mutualists such as pollinators indicate the need for additional empirical examinations.

Pollination manipulations

Our metaanalysis revealed that the type of cross influenced fitness differences between rare and common species ($QM = 9.96$, $df = 4$, $P = 0.041$; Fig. 3; Table S7). Rare species had reduced fecundity compared with their common congeners under hand-pollination and self-pollination (Fig. 3). Despite the limited numbers of studies ($n = 14$), the overall fail-safe number was high (fail-safe $n = 5490$, $P < 0.0001$) and the fail-safe ratio (68.6) passes Rosenthal's (1979) test, suggesting that these preliminary results could be robust, at least for hand-pollination and selfing treatments (Fig. 3). The funnel plot (Fig. S3) was significantly asymmetrical ($z = -4.28$, $P < 0.0001$), suggesting publication bias. We highlight that the main metaanalyses also include fecundity data from studies with unmanipulated flowers (open pollination); the low sample sizes of the open pollination studies here occurred only because we focused this metaanalysis on studies that explicitly manipulated some aspect of the mating system.

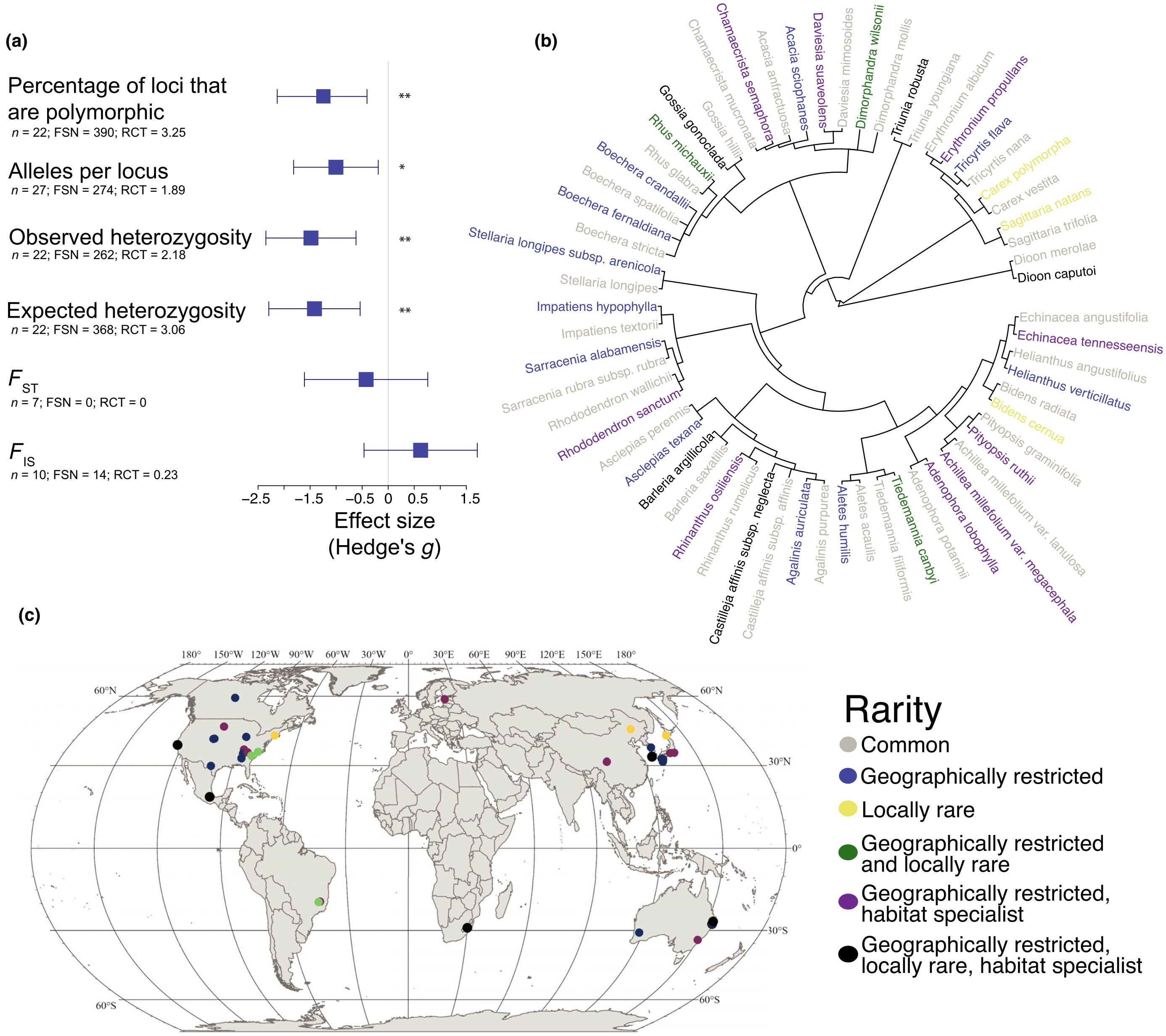

Fig. 1 (a) Population genetic metrics differed between rare and common congeners. Plotted are the estimates and 95% confidence intervals for the effect sizes (Hedge's g) of each population genetic parameter. In our metaanalysis, rare species had reduced population genetic diversity than their common congeners, as demonstrated by effect size values < 0 for the percentage of loci that were polymorphic, the number of alleles per locus, and the observed and expected heterozygosity. For each parameter, we indicate the fail-safe number (FSN), the number of studies (n) and Rosenthal's critical threshold (RCT). RCT values > 1 pass Rosenthal's test (see the Materials and Methods section). We assessed significance of effect sizes through Z-tests (*, $P < 0.05$; **, $P < 0.01$). (b) Phylogeny of rare and common species included in the metaanalysis, with taxa color-coded based on the rarity criteria used to classify each species. (c) Geographic distribution of studies included in the metaanalysis, color-coded based on the classification of the rare species. Rare species were contrasted with one or more common species in each location.

Discussion

Our metaanalyses revealed that rare species maintain lower population genetic diversity than their common congeners and have depressed fitness, smaller reproductive structures and possibly reduced survival. Our preliminary metaanalysis of pollination manipulation studies suggested that rare species also could suffer from reduced fertilization efficiency relative to common congeners. However, we did not detect broad differences in the functional traits of rare vs common species. Collectively, these results support our hypotheses about genetic diversity and fitness, but demonstrate our continued limited understanding of the ecoevolutionary factors associated with species rarity.

A metaanalysis of invasive species, as an extreme contrast to rare species, revealed that they express distinct suites of

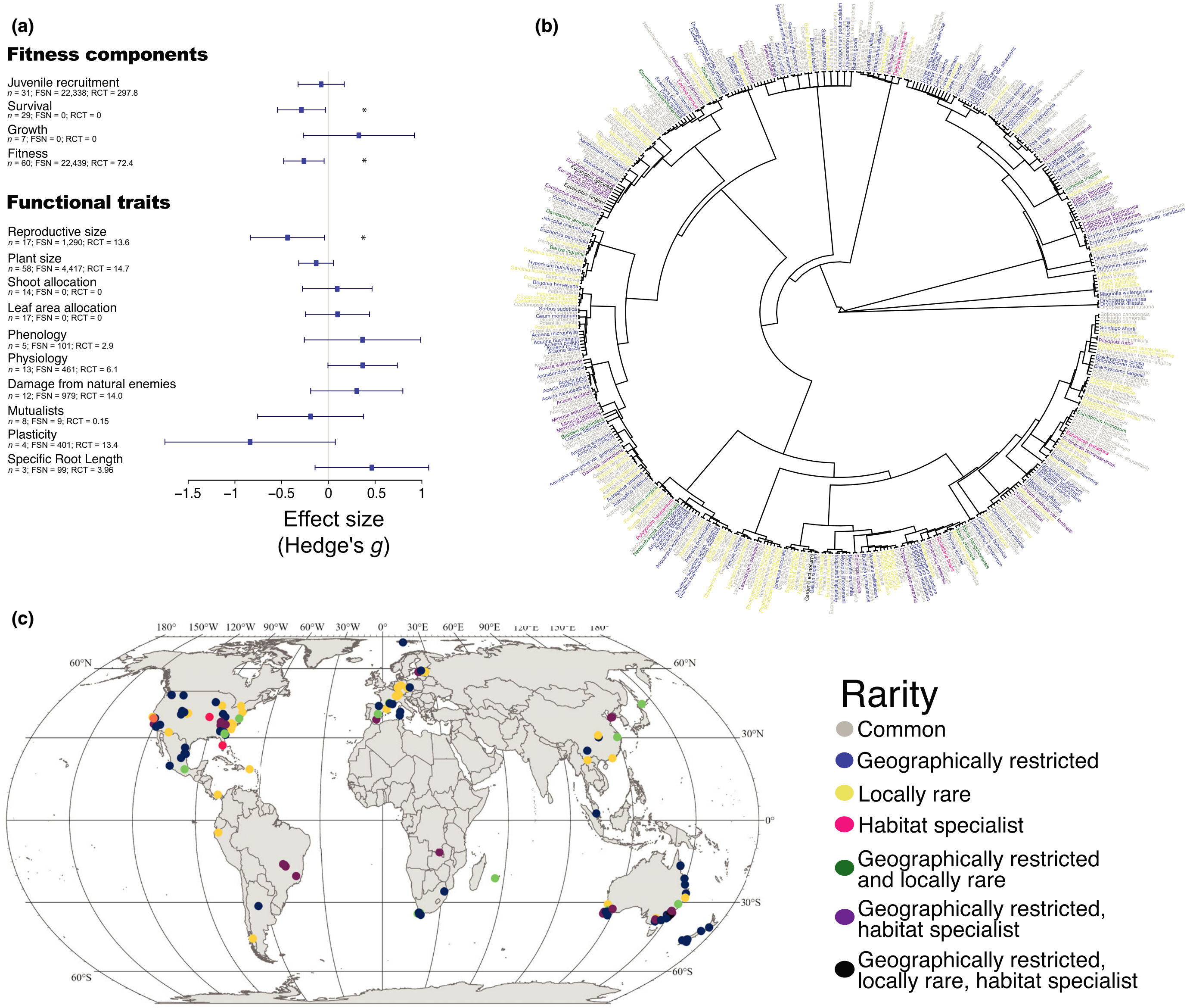

Fig. 2 (a) Metaanalysis of fitness and functional traits in a single combined analysis of binary and continuous datasets. Plotted are the estimates and 95% confidence intervals for the effect sizes (Hedge's *g*). Effect size values < 0 for fitness, survival and size of reproductive structures indicate that rare species underperformed relative to their common congeners. By contrast, the positive effect size for physiology suggests that rare species had greater physiological performance than their common congeners. For each parameter, we indicate the fail-safe number (FSN), the number of studies (*n*) and Rosenthal's critical threshold (RCT). RCT values > 1 pass Rosenthal's test (see the Materials and Methods section). We assessed significance of effect sizes through *Z*-tests (*, $P < 0.05$). (b) Phylogeny of rare and common species included in the metaanalysis, with taxa color-coded based on the rarity criteria used to classify each species. (c) Geographic distribution of studies included in the metaanalysis, color-coded based on the classification of the rare species. Rare species were contrasted with one or more common species in each location.

functional traits compared with native species (van Kleunen *et al.*, 2010). Many invasive species inhabit disturbed ecosystems (Catford *et al.*, 2012; Jauni *et al.*, 2015), and similarities in those systems, such as increased resource availability (Davis *et al.*, 2000), could favor traits generally associated with invasiveness, including rapid growth rates, high fecundity and highly efficient seed dispersal (Hamilton *et al.*, 2005; Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010). By contrast, species can be rare for many reasons, including their evolutionary history (Hodgson, 1986; Jetz *et al.*, 2004), specialization to rare habitats (Miller-Struttmann, 2013), biotic interactions such as competition or herbivory (Speed & Austrheim, 2017; Zhang & van Kleunen, 2019; Xi *et al.*, 2021), and/or anthropogenic factors including habitat loss and climate change (Lavergne *et al.*, 2005; Van Calster *et al.*, 2008; Harrison *et al.*, 2019). The myriad reasons underlying rarity could explain our findings of limited phenotypic differences.

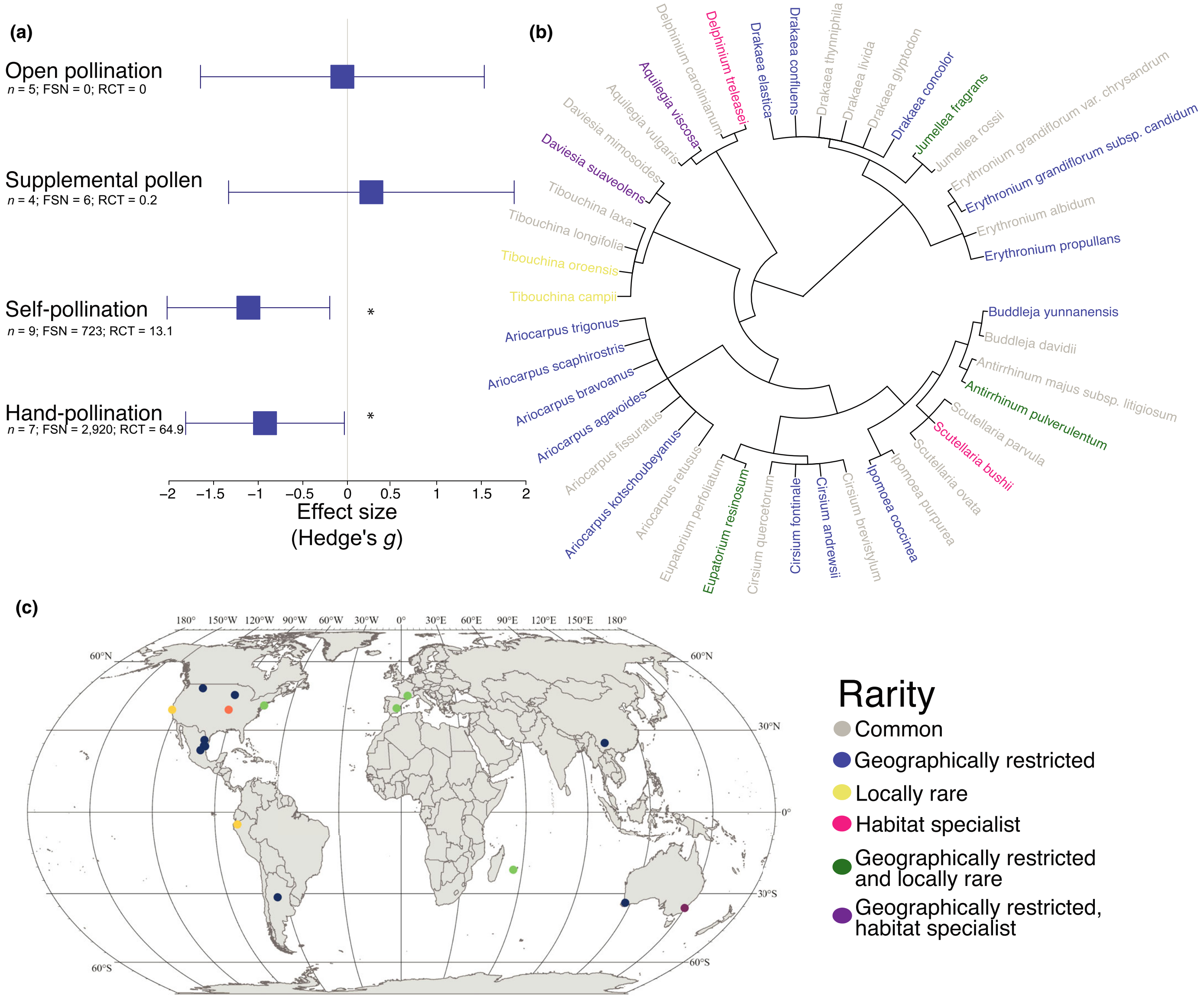

Fig. 3 (a) Meta-analysis of fecundity under separate mating system manipulations. Plotted are the estimates and 95% confidence intervals for the effect sizes (Hedge's *g*). Rare species had significantly lower fecundity when exposed to selfed pollen compared with their common congeners and when hand-pollinated with outcrossed pollen. For each parameter, we indicate the fail-safe number (FSN), the number of studies (*n*) and Rosenthal's critical threshold (RCT). RCT values > 1 pass Rosenthal's test (see the Materials and Methods section). The lack of significant patterns for open-pollination and supplemental pollination is probably due to limited numbers of studies contrasting rare and common congeners. We highlight the preliminary nature of this metaanalysis given the very low sample sizes of studies ($n = 14$) that manipulated some aspect of mating system dynamics. We assessed the significance of effect sizes through *Z*-tests (*, $P < 0.05$). (b) Phylogeny of rare and common species included in the metaanalysis, with taxa color-coded based on the rarity criteria used to classify each species. (c) Geographic distribution of studies included in the metaanalysis, color-coded based on the classification of the rare species. Rare species were contrasted with one or more common species in each location.

Distinctions among rarity types

Our understanding of rarity can be complicated by its various manifestations. The seven rarity types – as defined by geographic distribution, habitat specificity and local abundance (Rabinowitz, 1981) – could be associated with distinct ecoevolutionary causes and consequences (Murray *et al.*, 2002; Jiménez-Mejías *et al.*, 2015; Forrest *et al.*, 2017).

Geographic distribution Species with constrained geographic distributions probably maintain lower levels of genetic diversity than more widespread species (Hamrick & Godt, 1990), a finding supported by the results of our metaanalysis across rarity types. Our ability to draw nuanced conclusions about specific rarity types was limited by a bias toward studies of geographically restricted rare species in our metaanalysis. Species with wide distributions often have broad ecological niches, leading to the corollary that geographically restricted rare species inhabit relatively narrow niche spaces (Gaston, 2000; Slatyer *et al.*, 2013; Cardillo *et al.*, 2019). Niche breadth can be measured by assessing performance across a range of environmental conditions;

species with broad niches will experience less fitness variation across conditions than species with narrow niches (Sexton *et al.*, 2017). Although numerous studies of geographically restricted species in our datasets included abiotic treatments (Table S3), the vast majority did not describe niche breadth measures, such as fitness or performance curves or plasticity. Transplant experiments of rare species beyond their natural range could assess fundamental niche size relative to more common species (Sexton *et al.*, 2017).

Local abundance Low local abundance could constrain adaptation to environmental change given the reduced genetic variation associated with small populations (Ellstrand & Elam, 1993; Wagenius *et al.*, 2007; Leimu & Fischer, 2008; Hoffmann *et al.*, 2017), limit colonization of recently disturbed habitats and reduce competitive ability in later successional systems (Tilman, 1990; Levine & Rees, 2002; Zhang *et al.*, 2018). Life history traits such as greater stature, seed production and weight can enhance dispersal (Grime, 1974; Moles & Westoby, 2004; Thomson *et al.*, 2011), and self-fertilization can enable establishment in new locations (Pannell, 2015). Our results suggest that reduced fitness could impede the migration abilities of rare species. Two studies in our dataset contrasted the competitive abilities of locally rare and common congeners (Moora *et al.*, 2003; Moora & Jõgar, 2006), with both suggesting that rare *Viola elatior* is a poorer competitor than common *Viola mirabilis*. Research focused on the abilities of locally rare vs common species to adapt, migrate and compete could further our understanding of their abilities to establish and persist during rapid global change.

Habitat specificity Habitat specialists may have limited potential to migrate to new locations or adapt to novel conditions under climate change. However, specialists could be highly adapted to their native environments in ways that could enable them to outperform common congeners in those habitats. Many studies included in our metaanalyses applied experimental treatments for which ecological relevance was not always apparent, making it challenging to compare the effects of environmental factors on rare vs common species. Only eight studies (Osunkoya & Swanborough, 2001; Poot & Lambers, 2003a,b, 2008; Maliakal-Witt *et al.*, 2005; Powell & Knight, 2009; Ranieri *et al.*, 2012; Hirst *et al.*, 2017) included reciprocal transplant-like experiments that exposed both species to conditions relevant to the native environments of each. Reciprocal transplants in the field could investigate if rare habitat specialists are relegated to peripheral habitats because they are poor competitors in more prevalent habitat types or because they are well adapted to the conditions in marginal locations.

Complexities of rarity The majority of studies in our metaanalysis described species along a single dimension of rarity, limiting our ability to investigate the synergistic causes and consequences of restricted geographic ranges, low local abundance and narrow habitat specificity. Just eight studies reported on rare species characterized along all three dimensions of rarity (Tables S2, S3) As a result, our understanding of the rarest of species is extremely limited. We emphasize the need for additional studies examining the causes and consequences of rarity across multiple dimensions.

Approximately two-thirds of the studies included in our meta-analysis did not quantify rarity or provide information that would allow quantification (e.g. scaled range maps), precluding tests of how the extent of rarity influences genetic diversity, fitness and functional traits, and could guide the conservation of species of different rarity degrees. We encourage future studies to quantify rarity explicitly. For example, geographic distribution could be reported as the total area of occurrence (Lloyd *et al.*, 2002; Lovell & McKay, 2015), local abundance as the density of individuals or percentage cover in an area (Burne *et al.*, 2003; Egan *et al.*, 2014), and habitat specificity as frequency of occurrence in various habitat types (Wagner & Edwards, 2001) or density in the preferred habitat type relative to other habitat types (Oliver *et al.*, 2009).

Rare plant species are not evenly distributed across the Earth's surface (Enquist *et al.*, 2019). Distinct rarity hotspots occur in montane regions of the Americas, the Cape Floristic Region of South Africa, the Ethiopian Highlands, southwestern China and parts of Mediterranean Europe, among other locations (Enquist *et al.*, 2019). Such hotspots provide opportunities to investigate historical and contemporary drivers of rarity, and conservation efforts can target multiple species vulnerable to extinction. Rarity hotspots tend to occur in areas with high climate stability, and the rapid pace of contemporary climate change could threaten the persistence of rare species in these locations and elsewhere (Sandel *et al.*, 2011, 2017; Mouillot *et al.*, 2013; Enquist *et al.*, 2019). Future studies in rarity hotspots could investigate biological factors associated with rarity by comparing genetic and genomic diversity, fitness and functional traits of large numbers of diverse rare species, and investigate the responses of resident species to simulated climate change to examine extinction risks.

Implications for persistence through environmental change

Studies that examine the ecoevolutionary causes and consequences of rarity can help to elucidate the potential for rare species to persist through unprecedented environmental change due to human activities (Malhi *et al.*, 2020). To persist, species will need to adapt to novel selection *in situ* (Sheth *et al.*, 2018; Hamann *et al.*, 2021), acclimate to altered conditions (Chevin *et al.*, 2010; Nicotra *et al.*, 2010; Seebacher *et al.*, 2015) and/or migrate to suitable locations (Parmesan, 2006; Chen *et al.*, 2011; Pardi & Smith, 2012; Crickenberger & Wethey, 2018; Cazzolla Gatti *et al.*, 2019). Understanding how rare species could respond to future environmental change requires that studies manipulate the factors that are most likely to change (De Boeck *et al.*, 2015).

Adaptation Genetic drift, reduced mating opportunities, inbreeding depression, and increased demographic and genetic stochasticity can deplete genetic variation in small populations and restrict the adaptive potential of rare species (Ellstrand & Elam, 1993; Wagenius *et al.*, 2007; Leimu & Fischer, 2008; Luque *et al.*, 2016; Hoffmann *et al.*, 2017). Our findings that rare species have reduced population genetic diversity suggest that their ability to adapt to environmental change may be limited if genetic variability at neutral markers is correlated with variability at fitness-related markers. Owing to the historical nature of our dataset, population genetic parameters were measured via markers such as allozymes and microsatellites and were based on very few markers, representing a small fraction of the overall genome. Continued improvements in next-generation sequencing technologies hold great promise for identifying loci implicated in adaptation, assessing nucleotide diversity at those loci, examining the genomic signatures of demographic history, quantifying effective population size, evaluating the extent of populations genomic differentiation and gene flow, and examining rates of inbreeding (Fournier-Level *et al.*, 2011; Hoban *et al.*, 2016; Vallebueno-Estrada *et al.*, 2016; Bemmels *et al.*, 2019; Fitzpatrick *et al.*, 2021). Nevertheless, few studies have harnessed the power of sequence data to investigate the causes and consequences of rarity or to predict extinction risks (Helmstetter *et al.*, 2021).

To test whether limited genetic variation restricts the adaptive potential of rare species, quantitative genetic studies under ecologically realistic field conditions could estimate genetic variation in fitness and functional traits subject to selection. A recent analysis of tropical tree seedlings suggests that common species express trait values that are more adaptive than those expressed by rare species (Umaña *et al.*, 2015). Selection analyses (Rausher, 1992) that evaluate fitness as a function of functional traits under ecologically relevant conditions could test the hypothesis that locally rare or geographically restricted rare species are more poorly adapted, exhibiting trait values that fall farther from optimal values, than are common species. Furthermore, reciprocal transplant experiments could determine whether phenotypes of rare habitat specialists and common species are closer to the optimum in their respective home environments. Evolutionary genetic studies that evaluate quantitative genetic parameters in the context of global change (Etterson & Shaw, 2001; Bemmels & Anderson, 2019; Peschel *et al.*, 2021) could test whether common species maintain greater genetic variation in fitness than rare species in treatments that simulate future climates, and could examine whether genetic trade-offs across traits could restrict adaptation to environmental change (Etterson & Shaw, 2001). In particular, we call for manipulative studies that simulate projected future climates in field-based common garden experiments.

Acclimation Phenotypic plasticity could enable population persistence in the face of environmental change without genetic change (Nicotra & Davidson, 2010; Godoy *et al.*, 2012). Plant species can differ extensively in their plastic responses to environmental change (Sultan, 2000; Nicotra & Davidson, 2010; Godoy *et al.*, 2012; Dangremond *et al.*, 2015), and widespread species could have relatively high plasticity owing to greater spatial variation across their ranges (Murray *et al.*, 2002). Few studies explicitly contrasted plasticity across rare and common congeners (Liao *et al.*, 2006; Lovell & McKay, 2015; Hirst *et al.*, 2017; Rutherford *et al.*, 2017; Boyd *et al.*, 2022), even though numerous studies exposed rare and common species to multiple environmental conditions. Additionally, the plasticity studies in our dataset mostly neglected to test whether plasticity confers a fitness advantage in rare or common species (but see Boyd *et al.*, 2022), which is critical because plasticity can be a passive or maladaptive stress response (Palacio-López *et al.*, 2015; Hendry, 2016; Bonser, 2021). Studies that compare plasticity in rare and common species and link plasticity to performance in the context of probable environmental change could test the hypothesis that geographically restricted species or habitat specialists could be limited in their ability to acclimate to a broader range of environmental conditions.

Migration Migratory potential probably depends on species' abundance near existing range boundaries, which could impede the capacity for locally rare species to migrate in response to climate change (Iverson *et al.*, 2004) and constrain species distributions (Loveless & Hamrick, 1984). Limited flower, fruit and seed production and/or sizes also can restrict the dispersal potential of species (Angert *et al.*, 2011; Anderson, 2016; Schupp *et al.*, 2019; Schreiber & Beckman, 2020). The reduced fitness of rare species revealed by our metaanalyses (Fig. 2) could constrain their ability to migrate. Mismatches in the rapid ability of pollinator species to migrate relative to plant species (McKinney *et al.*, 2012; Gezon *et al.*, 2016; Richman *et al.*, 2020) could compound such effects, while extensive habitat fragmentation could further challenge migration in contemporary landscapes (Angert *et al.*, 2011). Although the influence of fragmentation on migration is not restricted to rare species (Dullinger *et al.*, 2015), species with low abundance are most susceptible to the genetic consequences of fragmentation (Reed & Frankham, 2003; Honnay & Jacquemyn, 2007).

Pollination manipulations Rare species could be limited by mating opportunities if populations are sparse and geographically disjointed, such that mates are few or pollinators infrequently visit flowers (Moeller, 2004; Benadi & Pauw, 2018). If rare and common congeners coexist, receipt of heterospecific pollen could further reduce fecundity in rare species (Ashman & Arceo-Gómez, 2013). However, these disadvantages could be offset by interspecific facilitation, as rare species can benefit from sharing pollinators with common species in diverse communities even when there is competition for pollinators (Moeller, 2004; Tur *et al.*, 2016; Benadi & Pauw, 2018; Bergamo *et al.*, 2020; Wei *et al.*, 2021). Our preliminary metaanalysis of mating systems revealed that rare species had reduced fecundity compared with their common congeners under self- and hand-pollination (Fig. 3), suggesting that they could experience reduced pollen germination and pollen tube growth or depressed efficiency of fertilization compared with their congeners. Alternatively, rare species may have reduced tolerance of floral manipulations, such as emasculation, relative to their common congeners. Our results could also be an artifact of variation in mating systems; for example, reduced seed set under selfing could have arisen if rare species are less self-compatible than their common congeners. We encourage future experiments to test the extent to which rare species may be limited by mating opportunities, and if the type of rarity influences mating system evolution. Studies that examine pollinator interactions and rates of inbreeding in rare species in the context of global declines in pollinator abundance and diversity (Biesmeijer *et al*., 2006; Williams *et al*., 2009; Burkle *et al*., 2013; Potts *et al*., 2016) will yield insights into their risk of extinction under global change.

Conclusions

Two decades ago, Bevill & Louda (1999) and Murray *et al.* (2002) reviewed plant life histories and traits in the context of species rarity and found very few patterns. These limited findings were attributed in part to a restricted body of autecological studies that measured different variables. By contrast, previous metaanalyses revealed that rare species tend to have lower levels of genetic diversity than their common congeners (Gitzendanner & Soltis, 2000; Cole, 2003). Our metaanalysis of a now larger body of research confirmed that rare species have reduced population genetic diversity and also revealed that rare species have depressed fitness relative to common congeners and could suffer from reduced efficiency of fertilization. However, we found few differences in functional traits. Discerning the ecological and evolutionary causes and consequences of rarity remains challenging, and our metaanalyses revealed persistent gaps in our understanding of species rarity. To fill those gaps, we advocate for ecologically relevant studies that examine additional elements of rarity, estimate quantitative genetic variation in fitness and functional traits, quantify the extent of adaptive phenotypic plasticity, evaluate the contributions of life history and mating system variation to rarity, and explicitly assess the potential for rare species to persist through global change via adaptation, acclimation and migration. Studies that examine the reasons for rarity could inform robust plans for the conservation of rare species and overall biodiversity against the pressures of contemporary environmental change.

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Author contributions

JNB and JTA conceived the project. JNB, JB, CB, JC-S and JTA extracted data for the analyses. JTA analyzed data. JNB and JTA wrote the first draft of the manuscript and prepared figures. All authors edited the manuscript. JNB and JTA contributed equally to this work.

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Data availability

The data that support the findings of this study and code used in this study are openly available in Dryad and Zenodo at 10.5061/dryad.3n5tb2rks.

References

Albert CH, Grassein F, Schurr FM, Vieilledent G, Violle C. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics* **13**: 217–225.

Anderson JT. 2016. Plant fitness in a rapidly changing world. *New Phytologist* **210**: 81–87.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species' traits predict recent shifts at expanding range edges?: traits and range shifts. *Ecology Letters* **14**: 677–689.

Ashman T, Arceo-Gómez G. 2013. Toward a predictive understanding of the fitness costs of heterospecific pollen receipt and its importance in co-flowering communities. *American Journal of Botany* **100**: 1061–1070.

Bemmels JB, Anderson JT. 2019. Climate change shifts natural selection and the adaptive potential of the perennial forb *Boechera stricta* in the Rocky Mountains. *Evolution* **73**: 2247–2262.

Bemmels JB, Knowles LL, Dick CW. 2019. Genomic evidence of survival near ice sheet margins for some, but not all, North American trees. *Proceedings of the National Academy of Sciences, USA* **116**: 8431–8436.

Benadi G, Pauw A. 2018. Frequency dependence of pollinator visitation rates suggests that pollination niches can allow plant species coexistence. *Journal of Ecology* **106**: 1892–1901.

Bergamo PJ, Susin Streher N, Traveset A, Wolowski M, Sazima M. 2020. Pollination outcomes reveal negative density-dependence coupled with interspecific facilitation among plants. *Ecology Letters* **23**: 129–139.

Bevill RL, Louda SM. 1999. Comparisons of related rare and common species in the study of plant rarity. *Conservation Biology* **13**: 493–498.

Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD *et al.* 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* **313**: 351–354.

Bonser SP. 2021. Misinterpreting the adaptive value of phenotypic plasticity in studies on plant adaptation to new and variable environments. *Plant Biology* **23**: 683–685.

Boyd JN, Odell J, Cruse-Sanders J, Rogers W, Anderson JT, Baskauf C, Brzyski J. 2022. Phenotypic plasticity and genetic diversity elucidate rarity and vulnerability of an endangered riparian plant. *Ecosphere* **13**: e3996. doi: 10.1002/ecs2.3996.

Bracken MES, Low NHN. 2012. Realistic losses of rare species disproportionately impact higher trophic levels: loss of rare 'cornerstone' species. *Ecology Letters* **15**: 461–467.

Burkle LA, Marlin JC, Knight TM. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science* **339**: 1611–1615.

Burne HM, Yates CJ, Ladd PG. 2003. Comparative population structure and reproductive biology of the critically endangered shrub *Grevillea althoferorum* and two closely related more common congeners. *Biological Conservation* **114**: 53–65.

Cardillo M, Dinnage R, McAlister W. 2019. The relationship between environmental niche breadth and geographic range size across plant species. *Journal of Biogeography* **46**: 97–109.

Catford JA, Daehler CC, Murphy HT, Sheppard AW, Hardesty BD, Westcott DA, Rejmánek M, Bellingham PJ, Pergl J, Horvitz CC *et al.* 2012. The intermediate disturbance hypothesis and plant invasions: implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics* **14**: 231–241.

Cazzolla Gatti R, Callaghan T, Velichevskaya A, Dudko A, Fabbio L, Battipaglia G, Liang J. 2019. Accelerating upward treeline shift in the Altai Mountains under last-century climate change. *Scientific Reports* **9**: 7678.

Chen I-C, Hill JK, Ohlemuller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* **333**: 1024–1026.

Chevin L-M, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS Biology* **8**: e1000357.

Chinn S. 2000. A simple method for converting an odds ratio to effect size for use in meta-analysis. *Statistics in Medicine* **19**: 3127–3131.

Cinar O, Nakagawa S, Viechtbauer W. 2022. Phylogenetic multilevel meta-analysis: a simulation study on the importance of modeling the phylogeny. *Methods in Ecology and Evolution* **13**: 383–395.

Cole CT. 2003. Genetic variation in rare and common plants. *Annual Review of Ecology, Evolution, and Systematics* **34**: 213–237.

Combs JK, Lambert AM, Reichard SH. 2013. Predispersal seed predation is higher in a rare species than in its widespread sympatric congeners (*Astragalus,* Fabaceae). *American Journal of Botany* **100**: 2149–2157.

Correa SB, de Oliveira PC, Nunes da Cunha C, Penha J, Anderson JT. 2018. Water and fish select for fleshy fruits in tropical wetland forests. *Biotropica* **50**: 312–318.

Crickenberger S, Wethey DS. 2018. Annual temperature variation as a time machine to understand the effects of long-term climate change on a poleward range shift. *Global Change Biology* **24**: 3804–3819.

Dangremond EM, Feller IC, Sousa WP. 2015. Environmental tolerances of rare and common mangroves along light and salinity gradients. *Oecologia* **179**: 1187–1198.

Darwin C. 1988. *On the origin of species, 1859.* Washington Square, NY, USA: New York University Press.

Davis MA, Grime JP, Thompson K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* **88**: 528–534.

De Boeck HJ, Vicca S, Roy J, Nijs I, Milcu A, Kreyling J, Jentsch A, Chabbi A, Campioli M, Callaghan T *et al.* 2015. Global change experiments: challenges and opportunities. *BioScience* **65**: 922–931.

Del Re AC. 2013. *compute.es: compute effect sizes. R package v.0.2-2.* [WWW document] URL http://cran.r-project.org/web/packages/compute.es [accessed 11 April 2022].

Domínguez Lozano F, Schwartz MW. 2005. Patterns of rarity and taxonomic group size in plants. *Biological Conservation* **126**: 146–154.

Dullinger S, Dendoncker N, Gattringer A, Leitner M, Mang T, Moser D, Mücher CA, Plutzar C, Rounsevell M, Willner W *et al.* 2015. Modelling the effect of habitat fragmentation on climate-driven migration of European forest understorey plants. *Diversity and Distributions* **21**: 1375–1387.

Egan JF, Graham IM, Mortensen DA. 2014. A comparison of the herbicide tolerances of rare and common plants in an agricultural landscape: herbicide tolerances of rare and common plants. *Environmental Toxicology and Chemistry* **33**: 696–702.

Ellstrand NC, Elam DR. 1993. Population genetic consequences of small population size: implications for plant conservation. *Annual Review of Ecology and Systematics* **24**: 217–242.

Enquist BJ, Feng X, Boyle B, Maitner B, Newman EA, Jørgensen PM, Roehrdanz PR, Thiers BM, Burger JR, Corlett RT *et al.* 2019. The commonness of rarity: global and future distribution of rarity across land plants. *Science Advances* **5**: eaaz0414.

Etterson JR, Shaw RT. 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**: 151–154.

Farnsworth E. 2007. Plant life history traits of rare versus frequent plant taxa of sandplains: implications for research and management trials. *Biological Conservation* **136**: 44–52.

Fitzpatrick MC, Chhatre VE, Soolanayakanahally RY, Keller SR. 2021. Experimental support for genomic prediction of climate maladaptation using the machine learning approach Gradient Forests. *Molecular Ecology Resources* **21**: 2749–2765.

Forrest A, Escudero M, Heuertz M, Wilson Y, Cano E, Vargas P. 2017. Testing the hypothesis of low genetic diversity and population structure in narrow endemic species: the endangered *Antirrhinum charidemi* (Plantaginaceae). *Botanical Journal of the Linnean Society* **183**: 260–270.

Fournier-Level A, Korte A, Cooper MD, Nordborg M, Schmitt J, Wilczek AM. 2011. A map of local adaptation in *Arabidopsis thaliana*. *Science* **334**: 86–89.

Frankham R. 2005. Genetics and extinction. *Biological Conservation* **126**: 131–140.

Futuyma DJ. 2010. Evolutionary constraint and ecological consequences. *Evolution* **64**: 1865–1884.

Gaston KJ. 2000. Global patterns in biodiversity. *Nature* **405**: 220–227.

Gezon ZJ, Inouye DW, Irwin RE. 2016. Phenological change in a spring ephemeral: implications for pollination and plant reproduction. *Global Change Biology* **22**: 1779–1793.

Gitzendanner MA, Soltis PS. 2000. Patterns of genetic variation in rare and widespread plant congeners. *American Journal of Botany* **87**: 783–792.

Godoy O, Valladares F, Castro-Díez P. 2012. The relative importance for plant invasiveness of trait means, and their plasticity and integration in a multivariate framework. *New Phytologist* **195**: 912–922.

Godt MJW, Hamrick JL. 2001. Genetic diversity in rare southeastern plants. *Natural Areas Journal* **21**: 61–70.

Grime JP. 1974. Vegetation classification by references to strategies. *Nature* **250**: 26–31.

Hadfield JD, Nakagawa S. 2010. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology* **23**: 494–508.

Hamann E, Pauli CS, Joly-Lopez Z, Groen SC, Rest JS, Kane NC, Purugganan MD, Franks SJ. 2021. Rapid evolutionary changes in gene expression in response to climate fluctuations. *Molecular Ecology* **30**: 193–206.

Hamilton MA, Murray BR, Cadotte MW, Hose GC, Baker AC, Harris CJ, Licari D. 2005. Life-history correlates of plant invasiveness at regional and continental scales: invasiveness at multiple spatial scales. *Ecology Letters* **8**: 1066–1074.

Hamrick J, Godt M. 1990. Allozyme diversity in plant species. In: Brown AHD, Clegg MT, Kahler AL, Weir BS, eds. *Plant population genetics, breeding, and genetic resources.* Sunderland, MA, USA: Sinauer, 43–63.

Harrer M, Cuijpers P, Furukawa T, Ebert DD. *DMETAR: companion R package for the guide 'doing meta-analysis in R'. R package v.0.0.9000.* [WWW document] URL https://dmetar.protectlab.org/ [accessed 11 April 2022].

Harrison T, Gibbs J, Winfree R. 2019. Anthropogenic landscapes support fewer rare bee species. *Landscape Ecology* **34**: 967–978.

Helmstetter AJ, Cable S, Rakotonasolo F, Rabarijaona R, Rakotoarinivo M, Eiserhardt WL, Baker WJ, Papadopulos AST. 2021. The demographic history of Madagascan micro-endemics: have rare species always been rare? *Proceedings of the Royal Society B: Biological Sciences* **288**: 20210957.

Hendry AP. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. *Journal of Heredity* **107**: 25–41.

Hinchliff CE, Smith SA, Allman JF, Burleigh JG, Chaudhary R, Coghill LM, Crandall KA, Deng J, Drew BT, Gazis R *et al.* 2015. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proceedings of the National Academy of Sciences, USA* **112**: 12764–12769.

Hirst MJ, Griffin PC, Sexton JP, Hoffmann AA. 2017. Testing the niche-breadth–range-size hypothesis: habitat specialization vs. performance in Australian alpine daisies. *Ecology* **98**: 2708–2724.

Hoban S, Kelley JL, Lotterhos KE, Antolin MF, Bradburd G, Lowry DB, Poss ML, Reed LK, Storfer A, Whitlock MC. 2016. Finding the genomic basis of local adaptation: pitfalls, practical solutions, and future directions. *The American Naturalist* **188**: 379–397.

Hodgson JG. 1986. Commonness and rarity in plants with special reference to the Sheffield flora part III: taxonomic and evolutionary aspects. *Biological Conservation* **36**: 275–296.

Hoffmann AA, Sgrò CM, Kristensen TN. 2017. Revisiting adaptive potential, population size, and conservation. *Trends in Ecology & Evolution* **32**: 506–517.

Honnay O, Jacquemyn H. 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. *Conservation Biology* **21**: 823–831.

Iverson LR, Schwartz MW, Prasad AM. 2004. How fast and far might tree species migrate in the eastern United States due to climate change? Migration of tree species due to climate change. *Global Ecology and Biogeography* 13: 209–219.

Jauni M, Gripenberg S, Ramula S. 2015. Non-native plant species benefit from disturbance: a meta-analysis. *Oikos* 124: 122–129.

Jetz W, Rahbek C, Colwell RK. 2004. The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecology Letters* 7: 1180–1191.

Jiménez-Mejías P, Fernández-Mazuecos M, Amat ME, Vargas P. 2015. Narrow endemics in European mountains: high genetic diversity within the monospecific genus *Pseudomisopates* (Plantaginaceae) despite isolation since the late Pleistocene. *Journal of Biogeography* 42: 1455–1468.

Karron JD. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically restricted and widespread plant congeners. *Evolutionary Ecology* 1: 47–58.

van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245.

Kraft NJB, Godoy O, Levine JM. 2015. Plant functional traits and the multidimensional nature of species coexistence. *Proceedings of the National Academy of Sciences, USA* 112: 797–802.

Krizek BA, Anderson JT. 2013. Control of flower size. *Journal of Experimental Botany* 64: 1427–1437.

Kunin WE, Gaston K. 1997. *The biology of rarity: causes and consequences of rare-common differences*. London, UK: Chapman & Hall.

Lajeunesse MJ. 2009. Meta-analysis and the comparative phylogenetic method. *The American Naturalist* 174: 369–381.

Lavergne S, Thompson JD, Garnier E, Debussche M. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos* 107: 505–518.

Lavergne S, Thuiller W, Molina J, Debussche M. 2005. Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region: environmental factors influencing the distribution of rare plants. *Journal of Biogeography* 32: 799–811.

Lawler JJ, White D, Sifneos JC, Master LL. 2003. Rare species and the use of indicator groups for conservation planning. *Conservation Biology* 17: 875–882.

Leimu R, Fischer M. 2008. A meta-analysis of local adaptation in plants. *PLoS ONE* 3: e4010.

Levine JM, Rees M. 2002. Coexistence and relative abundance in annual plant assemblages: the roles of competition and colonization. *The American Naturalist* 160: 452–467.

Liao J-X, Zou X-Y, Ge Y, Chang J. 2006. Effects of light intensity on growth of four *Mosla* species. *Botanical Studies* 47: 403–408.

Lloyd KM, Lee WG, Wilson JB. 2002. Growth and reproduction of New Zealand Acaena (Rosaceae) species in relation to rarity and commonness. *New Zealand Journal of Ecology* 26: 149–160.

Loveless MD, Hamrick JL. 1984. Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics* 15: 65–95.

Lovell JT, McKay JK. 2015. Ecological genetics of range size variation in *Boechera* spp. (Brassicaceae). *Ecology and Evolution* 5: 4962–4975.

Luque GM, Vayssade C, Facon B, Guillemaud T, Courchamp F, Fauvergue X. 2016. The genetic Allee effect: a unified framework for the genetics and demography of small populations. *Ecosphere* 7: e01413.

Lyons KG, Schwartz MW. 2001. Rare species loss alters ecosystem function – invasion resistance. *Ecology Letters* 4: 358–365.

MacArthur RH. 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences, USA* 43: 293–295.

Malhi Y, Franklin J, Seddon N, Solan M, Turner MG, Field CB, Knowlton N. 2020. Climate change and ecosystems: threats, opportunities and solutions. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 375: 20190104.

Maliakal-Witt S, Menges E, Denslow J. 2005. Microhabitat distribution of two Florida scrub endemic plants in comparison to their habitat-generalist congeners. *American Journal of Botany* 92: 411–421.

May R. 1999. Unanswered questions in ecology. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 354: 1951–1959.

McGill BJ, Etienne RS, Gray JS, Alonso D, Anderson MJ, Benecha HK, Dornelas M, Enquist BJ, Green JL, He F *et al.* 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10: 995–1015.

McKinney AM, CaraDonna PJ, Inouye DW, Barr B, Bertelsen CD, Waser NM. 2012. Asynchronous changes in phenology of migrating broad-tailed hummingbirds and their early-season nectar resources. *Ecology* 93: 1987–1999.

Michonneau F, Brown JW, Winter DJ. 2016. ROTL: an R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution* 7: 1476–1481.

Miller-Struttmann NE. 2013. Rarity and reproductive biology: habitat specialists reveal a complex relationship. *Botany-Botanique* 91: 349–359.

Moeller DA. 2004. Facilitative interactions among plants via shared pollinators. *Ecology* 85: 3289–3301.

Moora M, Sõber V, Zobel M. 2003. Responses of a rare (*Viola elatior*) and a common (*Viola mirabilis*) congeneric species to different management conditions in grassland – is different light competition ability responsible for difference abundances. *Acta Oecologica* 24: 169–174.

Moora M, Jõgar Ü. 2006. Competitive response of the rare *Viola elatior* and the common *Viola mirabilis*. *Plant Ecology* 184: 105–110.

Moles AT, Westoby M. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92: 372–383.

Mouillot D, Bellwood DR, Baraloto C, Chave J, Galzin R, Harmelin-Vivien M, Kulbicki M, Lavergne S, Lavorel S, Mouquet N *et al.* 2013. Rare species support vulnerable functions in high-diversity ecosystems. *PLoS Biology* 11: e1001569.

Munzbergova Z. 2005. Determinants of species rarity: population growth rates of species sharing the same habitat. *American Journal of Botany* 92: 1987–1994.

Murray BR, Thrall PH, Gill AM, Nicotra AB. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology* 27: 291–310.

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F *et al.* 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* 15: 684–692.

Nicotra AB, Davidson A. 2010. Adaptive phenotypic plasticity and plant water use. *Functional Plant Biology* 37: 117.

Oliver T, Hill JK, Thomas CD, Brereton T, Roy DB. 2009. Changes in habitat specificity of species at their climatic range boundaries. *Ecology Letters* 12: 1091–1102.

Osunkoya OO, Swanborough PW. 2001. Reproductive and ecophysiological attributes of the rare *Gardenia actinocarpa* (Rubiaceae) compared with its common co-occurring congener, *G. ovularis*. *Australian Journal of Botany* 49: 471.

Palacio-López K, Beckage B, Scheiner S, Molofsky J. 2015. The ubiquity of phenotypic plasticity in plants: a synthesis. *Ecology and Evolution* 5: 3389–3400.

Pannell JR. 2015. Evolution of the mating system in colonizing plants. *Molecular Ecology* 24: 2018–2037.

Paradis E, Schliep K. 2019. APE 5.0: an environment for modern phylogenetics and evolutionary anlyses in R. *Bioinformatics* 35: 526–528.

Pardi MI, Smith F. 2012. Paleoecology in an era of climate change: how the past can provide insights into the future. In: Louys J, ed. *Paleontology in ecology and conservation*. Berlin, Germany: Springer-Verlag, 93–116.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37: 637–669.

Peschel AR, Boehm EL, Shaw RG. 2021. Estimating the capacity of *Chamaecrista fasciculata* for adaptation to change in precipitation. *Evolution* 75: 73–85.

Poot P, Lambers H. 2003a. Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. *Journal of Ecology* 91: 58–67.

Poot P, Lambers H. 2003b. Growth responses to waterlogging and drainage of woody *Hakea* (Proteaceae) seedlings, originating from contrasting habitats in south-western Australia. *Plant and Soil* 253: 57–70.

Poot P, Lambers H. 2008. Shallow-soil endemics: adaptive advantages and constraints of a specialized root-system morphology. *New Phytologist* 178: 371–381.

Potts SG, Imperatriz-Fonseca V, Ngo HT, Aizen MA, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J *et al.* 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540: 220–229.

Powell KI, Knight TM. 2009. Effects of nutrient addition and competition on biomass of five *Cirsium* species (Asteraceae), including a serpentine endemic. *International Journal of Plant Sciences* **170**: 918–925.

Preston FW. 1948. The commonness, and rarity, of species. *Ecology* **29**: 254–283.

Pyšek P, Richardson DM. 2007. Traits associated with invasiveness in alien plants: where do we stand? In: Nentwig W, ed. *Ecological studies. Biological invasions*. Berlin & Heidelberg, Germany: Springer, 97–125.

Rabinowitz D. 1981. Seven forms of rarity. In: Synge H, ed. *The biological aspects of rare plant conservation*. Hoboken, NJ, USA: John Wiley & Sons, 205–207.

Rabinowitz D, Cairns S, Dillon T. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. In: Soule ME, ed. *Conservation biology: the science of scarcity and diversity*. Sunderland, MA, USA: Sinauer, 182–204.

Ranieri BD, Pezzini FF, Garcia QS, Chautems A, França MGC. 2012. Testing the regeneration niche hypothesis with Gesneriaceae (tribe Sinningiae) in Brazil: implications for the conservation of rare species. *Austral Ecology* **37**: 125–133.

Rausher MD. 1992. The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution* **46**: 616–626.

Reed DH, Frankham R. 2003. Correlation between fitness and genetic diversity. *Conservation Biology* **17**: 230–237.

Richman SK, Levine JM, Stefan L, Johnson CA. 2020. Asynchronous range shifts drive alpine plant-pollinator interactions and reduce plant fitness. *Global Change Biology* **26**: 3052–3064.

Rosenthal R. 1979. The file drawer problem and tolerance for null results. *Psychological Bulletin* **86**: 638–641.

Rutherford S, Bonser SP, Wilson PG, Rossetto M. 2017. Seedling response to environmental variability: the relationship between phenotypic plasticity and evolutionary history in closely related *Eucalyptus* species. *American Journal of Botany* **104**: 840–857.

Sandel B, Arge L, Dalsgaard B, Davies RG, Gaston KJ, Sutherland WJ, Svenning J-C. 2011. The influence of late Quaternary climate-change velocity on species endemism. *Science* **334**: 660–664.

Sandel B, Monnet A-C, Govaerts R, Vorontsova M. 2017. Late Quaternary climate stability and the origins and future of global grass endemism. *Annals of Botany* **119**: 279–288.

Schreiber SJ, Beckman NG. 2020. Individual variation in dispersal and fecundity increases rates of spatial spread. *AoB Plants* **12**: plaa001.

Schupp EW, Zwolak R, Jones LR, Snell RS, Beckman NG, Aslan C, Cavazos BR, Effiom E, Fricke EC, Montaño-Centellas F *et al.* 2019. Intrinsic and extrinsic drivers of intraspecific variation in seed dispersal are diverse and pervasive. *AoB Plants* **11**: plz067.

Seebacher F, White CR, Franklin CE. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* **5**: 61–66.

Sexton JP, Montiel J, Shay JE, Stephens MR, Slatyer RA. 2017. Evolution of ecological niche breadth. *Annual Review of Ecology, Evolution, and Systematics* **48**: 183–206.

Sheth SN, Kulbaba MW, Pain RE, Shaw RG. 2018. Expression of additive genetic variance for fitness in a population of partridge pea in two field sites. *Evolution* **72**: 2537–2545.

Slatyer RA, Hirst M, Sexton JP. 2013. Niche breadth predicts geographical range size: a general ecological pattern. *Ecology Letters* **16**: 1104–1114.

Song C, Peacor SD, Osenberg CW, Bence JR. 2020. An assessment of statistical methods for nonindependent data in ecological meta-analyses. *Ecology* **101**: e03184.

Speed JDM, Austrheim G. 2017. The importance of herbivore density and management as determinants of the distribution of rare plant species. *Biological Conservation* **205**: 77–84.

Stebbins GL. 1942. The genetic approach to problems of rare and endemic species. *Madrono* **6**: 241–258.

Stein BA, Kutner LS, Adams JS, Nature Conservancy (U.S.), Association for Biodiversity Information, eds. 2000. *Precious heritage: the status of biodiversity in the United States*. New York, NY, USA: Oxford University Press.

Sultan SE. 2000. Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science* **5**: 537–542.

Theodose TA, Jaeger CH, Bowman WD, Schardt JC. 1996. Uptake and allocation of ^{15}N in alpine plants: implications for the importance of competitive ability in predicting community structure in a stressful environment. *Oikos* **75**: 59.

Thomson FJ, Moles AT, Auld TD, Kingsford RT. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* **99**: 1299–1307.

Tilman D. 1990. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* **58**: 3.

Tur C, Sáez A, Traveset A, Aizen MA. 2016. Evaluating the effects of pollinator-mediated interactions using pollen transfer networks: evidence of widespread facilitation in south Andean plant communities. *Ecology Letters* **19**: 576–586.

Umaña MN, Zhang C, Cao M, Lin L, Swenson NG. 2015. Commonness, rarity, and intraspecific variation in traits and performance in tropical tree seedlings. *Ecology Letters* **18**: 1329–1337.

Valenta K, Nevo O. 2020. The dispersal syndrome hypothesis: how animals shaped fruit traits, and how they did not. *Functional Ecology* **34**: 1158–1169.

Vallebueno-Estrada M, Rodríguez-Arévalo I, Rougon-Cardoso A, Martínez González J, García Cook A, Montiel R, Vielle-Calzada J-P. 2016. The earliest maize from San Marcos Tehuacán is a partial domesticate with genomic evidence of inbreeding. *Proceedings of the National Academy of Sciences, USA* **113**: 14151–14156.

Van Calster H, Vandenberghe R, Ruysen M, Verheyen K, Hermy M, Decocq G. 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France: floristic changes in rural landscapes. *Journal of Ecology* **96**: 927–936.

Van Valen L. 1965. Morphological variation and width of ecological niche. *The American Naturalist* **99**: 377–390.

Viechtbauer W. 2010. Conducting meta-analyses in R with the METAFOR package. *Journal of Statistical Software* **36**: 1–48.

Wagenius S, Lonsdorf E, Neuhauser C. 2007. Patch aging and the S-allee effect: breeding system effects on the demographic response of plants to habitat fragmentation. *The American Naturalist* **169**: 383–397.

Wagner HH, Edwards PJ. 2001. Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology* **16**: 121–131.

Wei N, Kaczorowski RL, Arceo-Gómez G, O'Neill EM, Hayes RA, Ashman T-L. 2021. Pollinators contribute to the maintenance of flowering plant diversity. *Nature* **597**: 688–692.

Williams P, Colla S, Xie Z. 2009. Bumblebee vulnerability: common correlates of winners and losers across three continents. *Conservation Biology* **23**: 931–940.

Wright S. 1931. Evolution in Mendelian populations. *Genetics* **16**: 97–159.

Xi X, Zhou W, Li Z, Hu L, Dong Y, Niklas KJ, Sun S. 2021. Rare plant species are at a disadvantage when both herbivory and pollination interactions are considered in an alpine meadow. *Journal of Animal Ecology* **90**: 1647–1654.

Young AG, Brown AHD. 1996. Comparative population genetic structure of the rare woodland shrub *Daviesia suaveolens* and its common congener *D. mimosoides*. *Conservation Biology* **10**: 1220–1228.

Zavaleta ES, Hulvey KB. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* **306**: 1175–1177.

Zhang H, Qi W, Liu K. 2018. Functional traits associated with plant colonizing and competitive ability influence species abundance during secondary succession: evidence from subalpine meadows of the Qinghai-Tibetan Plateau. *Ecology and Evolution* **8**: 6529–6536.

Zhang Z, van Kleunen M. 2019. Common alien plants are more competitive than rare natives but not than common natives. *Ecology Letters* **22**: 1378–1386.

Supporting Information

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

Fig. S1 Funnel plot for metaanalysis of genetic diversity.

Fig. S2 Funnel plot for metaanalysis of fitness and functional traits.

Fig. S3 Funnel plot for metaanalysis of mating system dynamics.

Methods S1 Eligibility criteria, datasets and data extraction details.

Table S1 Bibliography of papers included in metaanalysis.

Table S2 Studies included in metaanalysis of genetic diversity.

Table S3 Studies included in metaanalysis of fitness and functional traits.

Table S4 Approaches of studies included in metaanalysis of fitness and functional traits.

Table S5 Results of metaanalysis of genetic diversity.

Table S6 Results of metaanalysis of fitness and functional traits.

Table S7 Results of metaanalysis of mating system.