Competition for pollinators destabilizes plant coexistence

https://doi.org/10.1038/s41586-022-04973-x

Received: 4 May 2021

Accepted: 13 June 2022

Christopher A. Johnson[1,2]✉, Proneet Dutt[2] & Jonathan M. Levine[1]

Mounting concern over the global decline of pollinators has fuelled calls for investigating their role in maintaining plant diversity[1,2]. Theory predicts that competition for pollinators can stabilize interactions between plant species by providing opportunities for niche differentiation[3], while at the same time can drive competitive imbalances that favour exclusion[4]. Here we empirically tested these contrasting effects by manipulating competition for pollinators in a way that predicts its long-term implications for plant coexistence. We subjected annual plant individuals situated across experimentally imposed gradients in neighbour density to either ambient insect pollination or a pollen supplementation treatment alleviating competition for pollinators. The vital rates of these individuals informed plant population dynamic models predicting the key theoretical metrics of species coexistence. Competition for pollinators generally destabilized the interactions between plant species, reducing the proportion of pairs expected to coexist. Interactions with pollinators also influenced the competitive imbalances between plant species, effects that are expected to strengthen with pollinator decline, potentially disrupting plant coexistence. Indeed, results from an experiment simulating pollinator decline showed that plant species experiencing greater reductions in floral visitation also suffered greater declines in population growth rate. Our results reveal that competition for pollinators may weaken plant coexistence by destabilizing interactions and contributing to competitive imbalances, information critical for interpreting the impacts of pollinator decline.

Ecologists have long recognized the importance of competition for abiotic resources in shaping plant diversity[5–7], and abundant empirical evidence has demonstrated that plants also compete for pollinators[8–10]. In fact, the vast majority of pollinators visit multiple plant species[11–13] such that co-flowering plants compete for the services of shared pollinators[10]. A key unresolved question, however, is how competition for pollinators affects plant coexistence. In a broader sense, coexistence depends on differences between species in how they interact with their abiotic and biotic environment. Termed ‘stabilizing niche differences’ in modern coexistence theory[7,14], these differences favour coexistence by causing individuals to harm individuals of the same species more strongly than they harm individuals of other species, which in turn benefits species dropping to low relative abundance. In this context, the beneficial and harmful effects of plants on the pollination of conspecific and heterospecific neighbours—collectively termed competition for pollinators[4,15,16]—can stabilize or destabilize plant interactions. For example, when different subsets of the pollinator community limit different plant species, competition for pollinators is hypothesized to favour plant coexistence by strengthening stabilizing niche differences[3]. Species dropping to low relative abundance experience weaker competition from conspecifics for pollinators, which benefits their population recovery. Another theory, however, predicts the exact opposite: competition for pollinators destabilizes plant competition by favouring common plant species over their rare competitors[15,16]. In this case, conspecific neighbours benefit one another by attracting pollinators and providing conspecific pollen. Plant species that drop to low relative abundance suffer because they attract fewer visits by pollinators or receive a greater fraction of heterospecific pollen due to previous pollinator visits to more common species.

Coexistence depends on the stabilizing niche differences between species exceeding the average fitness differences of species—their differential ability to grow and reproduce under limiting conditions[7]. These fitness differences simply favour one competitor over others regardless of their relative abundance, and drive competitive exclusion when they exceed the stabilizing niche difference[7]. In this context, a final mechanism by which competition for pollinators affects plant coexistence—rarely treated in theory—arises when pollen is limiting but plant species differ in their innate ability to attract pollinators and successfully transfer their pollen[4,17]. In such cases, competition for pollinators simply confers an advantage to some plant species over others, which, all else being equal, harms coexistence.

Critically, it has been exceedingly difficult to empirically disentangle these hypothesized effects of competition for pollinators, especially against the inevitable backdrop of competition for light and soil

---

[1]Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ, USA. [2]Institute of Integrative Biology, Swiss Federal Institute of Technology (ETH) Zürich, Zürich, Switzerland. ✉e-mail: cjohns21@uw.edu

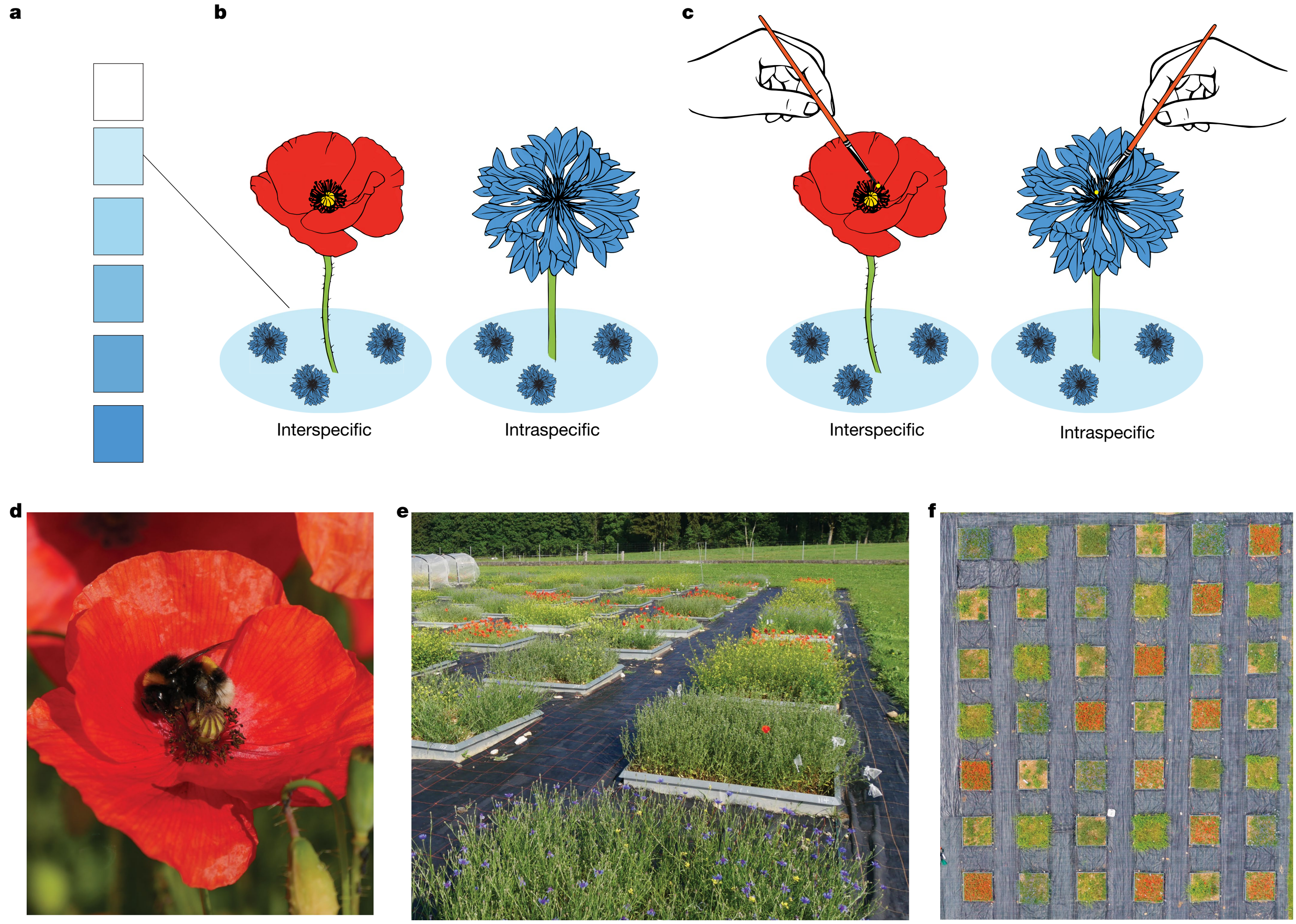


Fig. 1 | Hand pollination reveals the effects of competition for pollinators on plant coexistence. a–c, By supplementally hand pollinating focal individuals along a density gradient of background competitors (**a**), we quantified interspecific and intraspecific plant–plant interactions with competition for pollinators (**b**) and without competition for pollinators (**c**). **d–f**, In both treatments, plants interacted with ambient pollinators (**d**) and competed with background plant competitors within 80 2.25-m^2 plots (**e**) arranged within an approximately 650-m^2 study area (**f**) that mimicked a small, patchy meadow. Illustrations in **a**–**c** created by J. Johnson. Photographs in **d**–**f** taken by M. von Rütte.

resources. Fortunately, recent theoretical advances framing pollinator effects on plant diversity within modern coexistence theory[4] make it possible to empirically evaluate how competition for pollinators affects plant coexistence. Here we combine coexistence theory with field experiments to quantify the stabilizing niche and average fitness differences in the presence and absence of competition for pollinators, thereby quantifying the expected effect of competition for pollinators on plant coexistence.

We manipulated competition for pollinators between all pairs of five annual plant species characteristic of arable field margin communities in regions of Switzerland with dry, calcareous soils. Of these five species, only one (*Buglossoides arvensis*) is able to autonomously self-pollinate; the others rely obligately on pollinators (Extended Data Table 1). All of these plant species display generalized insect pollination syndromes and, in our study system, were visited most frequently by *Apis mellifera* and *Bombus terrestris* (family Apidae), with less-frequent visits from solitary bees (family Andrenidae) and Syrphid flies (family Syrphidae). We sowed focal individuals of each plant species into 80 2.25-m^2 plots within an approximately 650-m^2 area mimicking a small, patchy meadow (Fig. 1). Focal plants of each species competed against a single background competitor within a plot, and plots varied in the identity and density of the competitor species (Methods; Fig. 1). This experimental design allows us to parameterize population dynamic models of annual plant competition, from which we quantified the stabilizing niche difference and the average fitness difference between pairs of plant competitors. To experimentally disentangle the effects of competition for pollinators from other sources of plant competition, we quantified the stabilizing niche and average fitness differences under two treatments: one in which we supplementally hand-pollinated focal individuals so that species competed primarily for light and soil resources, but not for pollinators, and one in which plant species competed for the services of the ambient pollinator community in addition to these other resources (Fig. 1).

Our results countered the hypothesis that competition for pollinators provides an important axis of niche differentiation between plant species[3]. For nine of ten species pairs, competition for pollinators weakened stabilizing niche differences between competitors (Fig. 2a). Across all species pairs, competition for pollinators reduced the niche difference metric from an average of 0.296 to 0.023 (a 92% reduction; $t = 2.70$, d.f. = 9, $P = 0.024$; Supplementary Methods). These results support the hypothesis that pollinators destabilize plant competition by favouring more common plant species at the expense of their rarer competitors[15,16]. Competition for pollinators also had strong effects on the average fitness differences between plant species—imbalances that simply favour one competitor over others. In contrast to its consistent effects on stabilizing niche differences, however, competition for

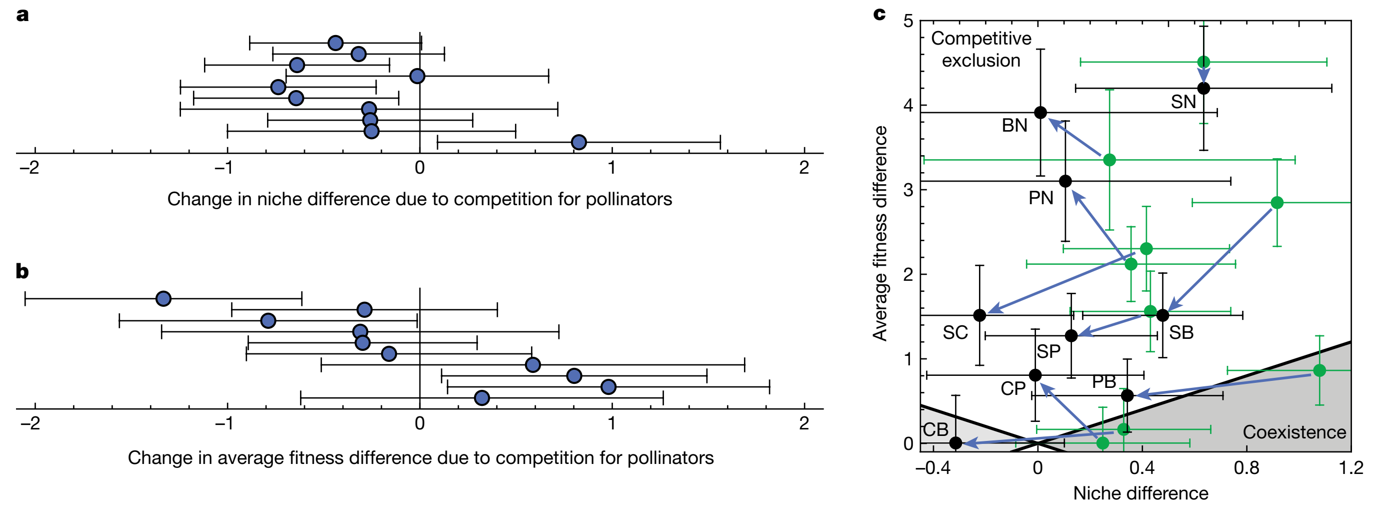


Fig. 2 | Effects of competition for pollinators on niche and average fitness differences. a,**b**, Changes in the stabilizing niche difference (**a**) and the average fitness difference (**b**) due to the effects of competition for pollinators. Each point corresponds to a species pair and points are stacked for visibility. **c**, Plant interaction outcomes predicted by the stabilizing niche and average fitness differences with (black points) and without (green points) competition for pollinators. Species coexist in the dark grey region, exclusion occurs in the white region, and a priority effect arises in the light grey region. Each arrow shows the overall effects of competition for pollinators on a given species pair, with the superior competitor listed first and the inferior competitor listed second. B, *B. arvensis*; C, *C. cyanus*; N, *N. arvensis*; P, *P. rhoeas*; S, *S. arvensis*. The *C. cyanus* and *N. arvensis* pair does not appear in **c** because its niche difference is extremely negative (−0.9 ± 0.6 and −1.7 ± 0.4 with and without competition for pollinators, respectively); this pair corresponds to the only positive point in **a**. The average fitness differences are plotted as ln(κ_2/κ_1), where species 2 is the superior competitor (for the *C. cyanus* and *N. arvensis* pair, ln(κ_C/κ_N) = 2.76 ± 0.81 and 2.44 ± 0.48 with and without competition for pollinators, respectively). Niche differences are plotted as −ln(ρ) to show each quantity on the same scale (Supplementary Methods). Plant coexistence requires that the average fitness difference, ln(κ_2/κ_1), is less than the stabilizing niche difference, −ln(ρ). In **a**–**c**, error bars show ±1 s.d.

pollinators accentuated and weakened the average fitness difference between plant species pairs to roughly equal degrees, generating no significant average effect (Fig. 2b; $t = 1.02$, d.f. = 9, $P = 0.33$).

Long-term stable co-occurrence of species is predicted when the stabilizing niche difference between a pair of species exceeds the average fitness difference, as depicted by the dark grey region in Fig. 2c. Outside this region, one species excludes the other. Consistent with its destabilizing effects and its potential to augment average fitness differences, competition for pollinators never permitted plant coexistence (Fig. 2c). In fact, competition for pollinators disrupted the coexistence of all three species pairs predicted to coexist in the absence of pollen limitation: *Papaver rhoeas* and *B. arvensis* (PB in Fig. 2c), *Centaurea cyanus* and *B. arvensis* (CB in Fig. 2c) and *C. cyanus* and *P. rhoeas* (CP in Fig. 2c). All other pairs were predicted to show exclusion even without pollen limitation, and the majority of these pairs were predicted to move even further from the coexistence region with competition for pollinators. Given an expectation of three of ten species pairs predicted to coexist without pollen limitation, our finding that zero of ten species pairs are predicted to coexist with competition for pollinators is significantly less than expected under random chance (exact binomial test: $n = 10$, $k = 0.3$, $P = 0.039$), suggesting that competition for pollinators significantly reduced plant coexistence.

Reduced intraspecific limitation—a result consistent with large floral displays disproportionately increasing pollination of conspecifics—underlies much of the destabilizing effects of competition for pollinators. Three of five species were proven to be pollen limited without neighbours (*P. rhoeas*, *C. cyanus* and *Nigella arvensis*), such that their low-density fecundity was roughly three times greater when hand pollinated (Fig. 3a and Extended Data Table 2). For these species, intraspecific limitation—which stabilizes coexistence—was greatly reduced under ambient versus hand pollination (blue panels in Fig. 3b; although not significantly so for *N. arvensis*), and these three intraspecific interactions contributed to the niche differences for nine of ten pairs. This result is consistent with beneficial effects of conspecific neighbours on pollination through the creation of more attractive floral displays or the greater provisioning of conspecific (versus heterospecific) pollen, both of which would counter competition from conspecific neighbours for other resources. Conversely, competition for pollinators had variable effects on suppression by heterospecific neighbours (white panels in Fig. 3b), pointing to its weakening of intraspecific limitation as the major driver of our finding that competition for pollinators weakened stabilizing niche differences.

Although all of these results concern neighbour effects at very local spatial scales, pollinators forage over larger spatial scales than our plots[18], possibly influencing the estimated values and uncertainties of our fitted model parameters. Indeed, diffuse competition for pollinators with plants in the broader experimental landscape probably explains the pollen limitation of plants with no local competitors in the same plot (Fig. 3a). Nonetheless, in the Supplementary Discussion, we show that local competition for pollinators with plants in the same plot is the overwhelming determinant of our results. Moreover, we found that, although pollen limitation of the four self-incompatible species was affected by the identity of the competitor species within its same plot, it was unaffected by the abundance of the different competitor species at successively larger spatial scales (Extended Data Table 3), suggesting that the identity of the competitor for pollinators most prominently mattered at the local scale of our plots.

Our results reveal that competition for pollinators destabilizes plant coexistence and contributes to competitive imbalances, information that is critical for interpreting the effects of pollinator decline on plant diversity[1,19]. Specifically, our findings emphasize that pollinator effects on plant fitness differences can be substantial (Fig. 2b), effects that should grow even stronger if pollinator decline leads to greater pollen limitation[1,2]. To investigate this hypothesis, we experimentally simulated pollinator decline by enclosing replicate 2.25-m^2 communities of the five plant species with only a single pollinator species (*B. terrestris*),

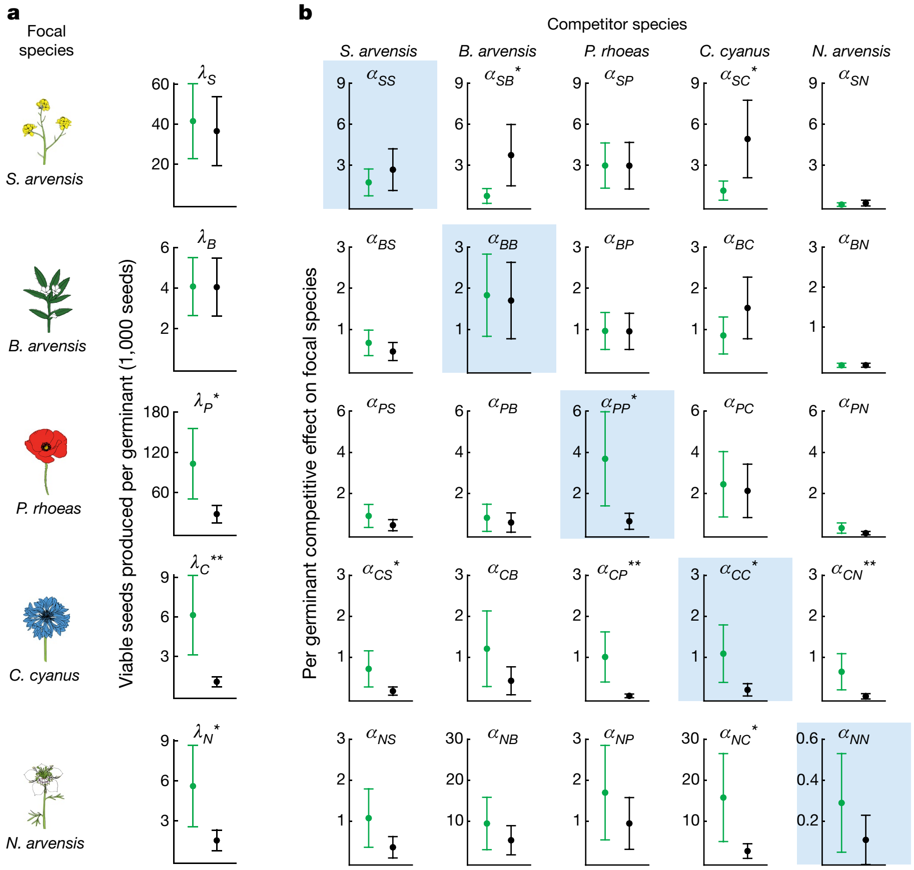


Fig. 3 | Effects of competition for pollinators on parameter estimates. **a**,**b**, Low-density fecundity, λ_i (**a**), and competition coefficents, α_{ij} (**b**), describing the per capita effect of species j (columns) on focal species i (rows). The black and green points are parameter estimates (±s.e.) with and without competition for pollinators, respectively. The blue boxes indicate intraspecific interactions. Note that in the annual plant competition model that we used to predict interaction outcomes, the conditions $\alpha_{ii} > \alpha_{ji}$ and $\alpha_{jj} > \alpha_{ij}$ favour, but do not guarantee, coexistence (Supplementary Methods). The asterisks (*) and double asterisks (**) signify that the estimates are significantly different at the $P < 0.1$ and $P < 0.05$ level, respectively (likelihood-ratio tests; two-sided; $n = 13$ parameters; see Extended Data Table 2). Illustrations in **a** created by J. Johnson.

and as a control, subjected the same plant community to open enclosures accessible to the ambient pollinator community (Methods). The reduction in visitation with pollinator decline differed across the five species (x axis in Fig. 4). Moreover, the effect of pollinator decline on the per capita population growth rates of the plant species was well predicted by the reduction in their visitation (Fig. 4). These results extend recent findings[20,21] to our system, and suggest that pollinator declines could differentially impact plant performance, favouring some competitors over others.

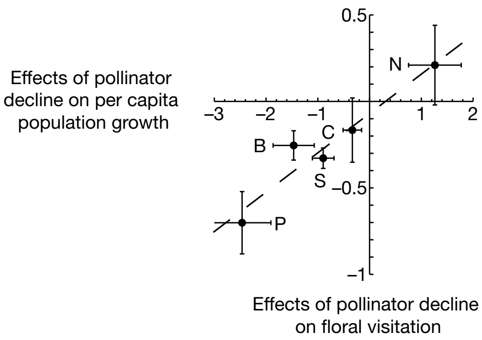


Fig. 4 | Effects of experimentally simulated pollinator decline on floral visitation and plant per capita population growth. Log-ratios of the mean floral visitation and the mean per capita population growth rate under pollinator decline ($n = 10$ plots) relative to the ambient pollinator community ($n = 12$ plots) for each plant species (Supplementary Methods). Error bars show s.e. The dashed line is the line of best fit of a least-squares linear regression (two-sided; $n = 5$ species; $t = 5.25$; $P = 0.01$).

Our central finding that competition for pollinators tends to destabilize plant interactions comes with important distinctions and caveats. First, and as a matter of context, biologists have long known that plant species differentially rely on pollinators[22,23], and thus the presence or absence of pollinators should naturally influence plant competitors. However, this general effect of pollinators is different than the specific role of competition for pollinators on plant coexistence, as examined here. Indeed, recent work has compared plant interactions in the presence and absence of pollinators in synthetic communities, and shown that pollinators increase plant persistence probability through direct and indirect interactions[24]. By contrast, we experimentally alleviated pollen limitation while leaving the natural pollinator community intact to specifically quantify the effects of competition for these pollinators. Along these lines, we acknowledge that our hand pollination treatment might not have completely eliminated competition for pollinators, but if so, our results would underestimate the true destabilizing effects of this interaction.

A second consideration is that our study specifically captures pollinator foraging decisions at spatial scales smaller than the 650-m^2 scale of our experiment. How competition for pollinators at even large spatial scales influences competition among neighbouring species is an important question worthy of further study, probably requiring the integration of plant effects on pollinator demography. More generally, our study did not explicitly consider coexistence mechanisms of plant species operating over larger spatial and temporal scales[7], probably explaining why local coexistence was predicted to be rare in our annual plant community at the plot scale. Finally, competition for pollinators could, in principle, enable coexistence in a more diverse community, even when destabilizing individual species pairs, for example, by driving intransitive loops in competitive dominance[25]. Our central result that competition for pollinators tends to reduce niche differences always held when we used a structural stability approach[26] to examine the effects of pairwise competition for pollinators in all three-species, four-species and five-species communities, and simulations confirmed that the outcome of the pairwise interactions (Fig. 2c) were unchanged in these more speciose plant communities (Extended Data Table 4).

Pollinator decline is expected to make pollen increasingly limiting[1], and this loss of mutualism has long been expected to harm plant demographic performance[2,24]. However, greater pollen limitation also implies greater competition for pollinators. Our central finding that competition for pollinators generally destabilizes plant coexistence predicts that pollinator decline may also degrade plant diversity through the erosion of stabilizing niche differences. Furthermore, although past theoretical studies have not emphasized pollinator effects on plant average fitness differences (but see refs. [4,17]), our empirical investigation demonstrates that these effects can be quite substantial. The accentuating or equalizing effects of competition for pollinators on plant average fitness differences should grow even stronger with pollinator decline, changing interaction outcomes in ways that are difficult to predict. Indeed, our experimentally simulated pollinator decline led to severe reductions in both floral visitation and per capita seed production that favoured some plant competitors over others. More generally, our study lays the groundwork for more theoretically robust investigations of how pollinators affect plant diversity, studies that are critical for understanding the maintenance of biodiversity and predicting the coexistence consequences of global declines in pollinators.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-022-04973-x.

1. Potts, S. et al. Global pollinator declines: trends, impacts and drivers. *Trends Ecol. Evol.* **25**, 345–353 (2010).
2. Thomann, M., Imbert, E., Devaux, C. & Cheptou, P.-O. Flowering plants under global pollinator decline. *Trends Plant Sci.* **18**, 353–359 (2013).
3. Pauw, A. Can pollination niches facilitate plant coexistence? *Trends Ecol. Evol.* **28**, 30–37 (2013).
4. Johnson, C. A. How mutualisms influence the coexistence of competing species. *Ecology* **102**, e03346 (2021).
5. Tilman, D. *Resource Competition and Community Structure* (Princeton Univ. Press, 1982).
6. Tilman, D. Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* **58**, 3–15 (1990).
7. Chesson, P. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**, 343–358 (2000).
8. Mitchell, R. J., Flanagan, R. J., Brown, B. J., Waser, N. M. & Karron, J. D. New frontiers in competition for pollination. *Ann. Bot.* **103**, 1403–1413 (2009).
9. Morales, C. L. & Traveset, A. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* **12**, 716–728 (2009).
10. Jones, E. I., Bronstein, J. L. & Ferrière, R. The fundamental role of competition in the ecology and evolution of mutualisms. *Ann. N. Y. Acad. Sci.* **1256**, 66–88 (2012).
11. Memmott, J., Waser, N. M. & Price, M. V. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B* **271**, 2605–2611 (2004).
12. Bascompte, J. & Jordano, P. *Mutualistic Networks* (Princeton University Press, 2013).
13. Bascompte, J. Mutualism and biodiversity. *Curr. Biol.* **29**, R467–R470 (2019).
14. Chesson, P. Updates on mechanisms of maintenance of species diversity. *J. Ecol.* **106**, 1773–1794 (2018).
15. Levin, D. A. & Anderson, W. W. Competition for pollinators between simultaneously flowering species. *Am. Nat.* **104**, 455–467 (1970).
16. Kunin, W. & Iwasa, Y. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. *Theor. Popul. Biol.* **49**, 232–263 (1996).
17. Lanuza, J. B., Bartomeus, I. & Godoy, O. Opposing effects of floral visitors and soil conditions on the determinants of competitive outcomes maintain species diversity in heterogeneous landscapes. *Ecol. Lett.* **21**, 865–874 (2018).
18. Thomson, J. Spatial and temporal components of resource assessment by flower-feeding insects. *J. Anim. Ecol.* **50**, 49–59 (1981).
19. Knight, T. M. et al. Reflections on, and visions for, the changing field of pollination ecology. *Ecol. Lett.* **21**, 1282–1295 (2018).
20. Biella, P. et al. Experimental loss of generalist plants reveals alterations in plant-pollinator interactions and a constrained flexibility of foraging. *Sci. Rep.* **9**, 7376 (2019).
21. Brosi, B. & Briggs, H. M. Single pollinator species losses reduce floral fidelity and plant reproductive function. *Proc. Natl Acad. Sci. USA* **110**, 13044–13048 (2013).
22. Addicott, J. F. in *The Biology of Mutualism* (ed. Boucher, D. H.) 217–247 (Croom Helm, 1985).
23. Knight, T. M. et al. Pollen limitation of plant reproduction: pattern and process. *Annu. Rev. Ecol. Evol. Syst.* **36**, 467–497 (2005).
24. Bartomeus, I., Saavedra, S., Rohr, R. P. & Godoy, O. Experimental evidence of the importance of multitrophic structure for species persistence. *Proc. Natl Acad. Sci. USA* **118**, e2023872118 (2021).
25. Levine, J. M., Bascompte, J., Adler, P. B. & Allesina, S. Beyond pairwise mechanisms of species coexistence in complex communities. *Nature* **546**, 56–64 (2017).
26. Saavedra, S. et al. A structural approach for understanding multispecies coexistence. *Ecol. Monogr.* **87**, 470–486 (2017).

Methods

Field setup and experimental manipulation of competition for pollinators

We studied five common annual plant species commonly found in field margins in dry, hilly, calcareous soil regions of Switzerland. The species are *Sinapis arvensis*, *B. arvensis*, *P. rhoeas*, *C. cyanus* and *N. arvensis* (Extended Data Table 1). Field work was conducted at the Eschikon-Lindau Field Station of the ETH Zürich, Switzerland, in an approximately 650-m^2 area containing the 80 2.25-m^2 plots used in our study. The sample sizes were determined by the number of available plots, with 10 focal individuals per plot (Supplementary Methods). Blinding was not possible in this study. Focal individuals of each plant species competed against a single background competitor within each plot, which varied in the identity and density of the competitor species. Focal individuals were randomly assigned positions within a plot and background competitor species were randomly assigned to the plots, ensuring only that the same species was not sown in directly neighbouring plots to minimize highly clumped floral displays across plots. We measured the per capita seed production of each species as a function of the number of germinated neighbours that it faced within a 20-cm radius (Supplementary Methods). Two focal plants per species per plot were randomly assigned to one of two treatments: supplemental hand pollination and a control treatment in which plants received only ambient pollination.

Field parameterization of population models

We field-parameterized a mathematical model describing the population dynamics of competing annual plants, using instrumental variables analysis to account for omitted variable bias[27] (Supplementary Methods). The parameterized model was used to estimate stabilizing niche differences and average fitness differences between all pairs of competitors and to predict interaction outcomes (Supplementary Methods). We used likelihood-ratio tests to compare model estimates of each parameter between the two pollination treatments.

Experimentally simulated pollinator decline

We experimentally simulated pollinator decline by enclosing an additional 22 replicate 2.25-m^2 plots sown with all five plant species, and then subjected these communities to one of two randomly assigned pollinator treatments. In the pollinator decline treatment, we maintained only a single pollinator species (one male *B. terrestris*), and in the control, the communities were accessible to the ambient pollinator community. We observed floral visits under both pollinator treatments and estimated the per capita seed production of each species (Supplementary Methods).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this paper.

Data availability

Data are available on Zenodo: https://doi.org/10.5281/zenodo.6474018. The data were recorded in Microsoft Excel (v. 16.48) and analysed in R (v. 3.6.3). Source data are provided with this paper.

Code availability

Codes are available on Zenodo: https://doi.org/10.5281/zenodo.6474018. The figures were plotted in Mathematica (v. 12.0).

27. Rinella, M. J., Strong, D. J. & Vermeire, L. T. Omitted variable bias in studies of plant interactions. *Ecology* **101**, e03020 (2020).

Acknowledgements We thank M. von Rütte, A. Bieger, C. Hess, M. Negreiros, A. Reid and R. Zäch for their work in the field and laboratory; J. Johnson (Life Science Studios) for the illustrations in Figs. 1 and 3; W. Petry and S. Hart for statistical advice; and laboratory members at the ETH Zürich and Princeton University for comments on the manuscript. C.A.J. was supported by the ETH Zürich Center for Adaptation to Changing Environments and funds from Princeton University. J.M.L. was supported by NSF grant DEB 2022213.

Author contributions C.A.J. and J.M.L. designed the research. C.A.J. performed the experiments and analysed the data. P.D. and C.A.J. conducted the pollinator observations. C.A.J. and J.M.L. wrote the manuscript.

Competing interests The authors declare no competing interests.

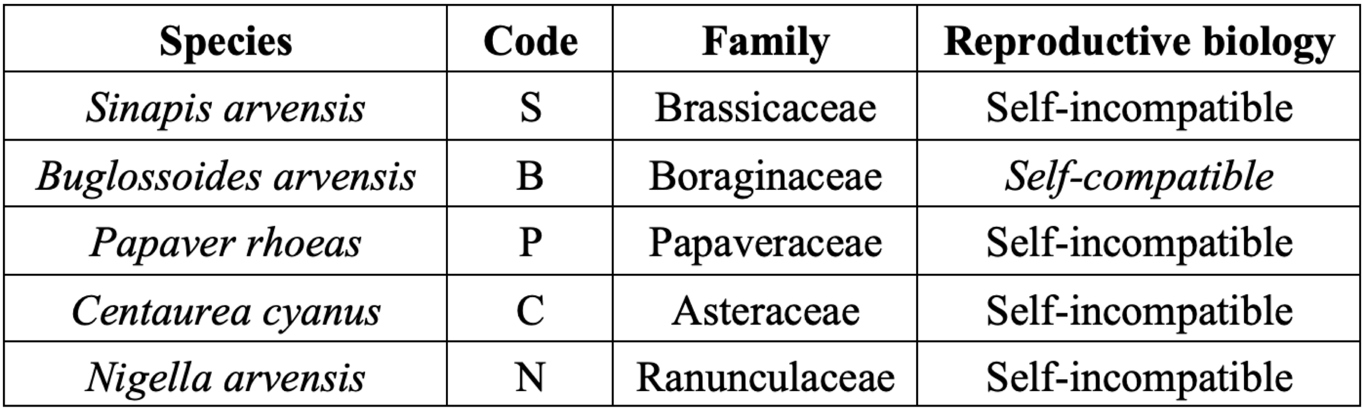
Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41586-022-04973-x.

Correspondence and requests for materials should be addressed to Christopher A. Johnson.

Peer review information *Nature* thanks Peter Chesson and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

Extended Data Table 1 | Details about the annual plant species used in the experiment



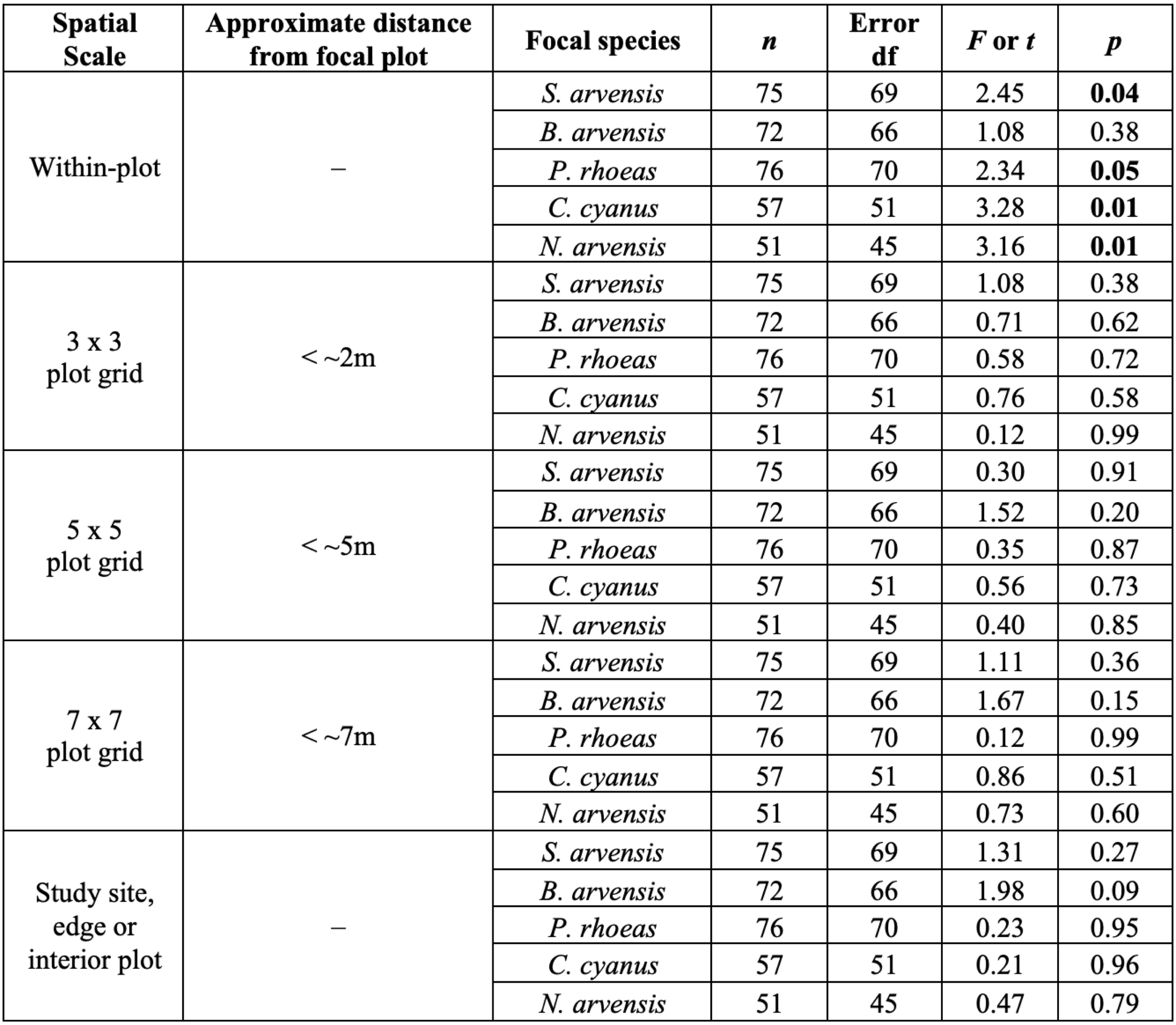
Species	Code	Family	Reproductive biology
Sinapis arvensis	S	Brassicaceae	Self-incompatible
Buglossoides arvensis	B	Boraginaceae	*Self-compatible*
Papaver rhoeas	P	Papaveraceae	Self-incompatible
Centaurea cyanus	C	Asteraceae	Self-incompatible
Nigella arvensis	N	Ranunculaceae	Self-incompatible

Extended Data Table 2 | Likelihood-ratio tests evaluating whether low-density fecundity, λ_i, or competition coefficients, α_{ij}, differed between pollination treatments

Focal species	Low-density fecundity, λ_i	Competition coefficient, α_{ij}				
		S. arvensis	*B. arvensis*	*P. rhoeas*	*C. cyanus*	*N. arvensis*
S. arvensis	$\chi^2 = 0.04$ $p = 0.84$	$\chi^2 = 0.32$ $p = 0.57$	$\chi^2 = 3.66$ $p = 0.06$	$\chi^2 = 0.00004$ $p = 0.99$	$\chi^2 = 3.44$ $p = 0.06$	$\chi^2 = 0.21$ $p = 0.65$
B. arvensis	$\chi^2 = 0.0003$ $p = 0.99$	$\chi^2 = 0.30$ $p = 0.59$	$\chi^2 = 0.009$ $p = 0.93$	$\chi^2 = 0.0005$ $p = 0.98$	$\chi^2 = 0.61$ $p = 0.43$	$\chi^2 = 0.0009$ $p = 0.98$
P. rhoeas	$\chi^2 = 3.40$ $p = 0.07$	$\chi^2 = 0.64$ $p = 0.42$	$\chi^2 = 0.08$ $p = 0.77$	$\chi^2 = 4.00$ $p = 0.05$	$\chi^2 = 0.02$ $p = 0.87$	$\chi^2 = 1.30$ $p = 0.26$
C. cyanus	$\chi^2 = 7.80$ $p = 0.005$	$\chi^2 = 3.06$ $p = 0.08$	$\chi^2 = 0.96$ $p = 0.33$	$\chi^2 = 7.30$ $p = 0.007$	$\chi^2 = 3.23$ $p = 0.07$	$\chi^2 = 4.63$ $p = 0.03$
N. arvensis	$\chi^2 = 3.25$ $p = 0.07$	$\chi^2 = 1.39$ $p = 0.24$	$\chi^2 = 0.39$ $p = 0.53$	$\chi^2 = 0.40$ $p = 0.53$	$\chi^2 = 3.81$ $p = 0.05$	$\chi^2 = 0.58$ $p = 0.45$

We used likelihood-ratio tests (with d.f. = 12) to compare a full model with separate estimates of the parameters for each treatment with a reduced model with only one estimate of the parameter across both treatments (Supplementary Methods).

Extended Data Table 3 | Effects of plant competitors for pollinators at multiple spatial scales on pollen limitation



Spatial Scale	Approximate distance from focal plot	Focal species	*n*	Error df	*F* or *t*	*p*
Within-plot	–	*S. arvensis*	75	69	2.45	**0.04**
		B. arvensis	72	66	1.08	0.38
		P. rhoeas	76	70	2.34	**0.05**
		C. cyanus	57	51	3.28	**0.01**
		N. arvensis	51	45	3.16	**0.01**
3 x 3 plot grid	< ~2m	*S. arvensis*	75	69	1.08	0.38
		B. arvensis	72	66	0.71	0.62
		P. rhoeas	76	70	0.58	0.72
		C. cyanus	57	51	0.76	0.58
		N. arvensis	51	45	0.12	0.99
5 x 5 plot grid	< ~5m	*S. arvensis*	75	69	0.30	0.91
		B. arvensis	72	66	1.52	0.20
		P. rhoeas	76	70	0.35	0.87
		C. cyanus	57	51	0.56	0.73
		N. arvensis	51	45	0.40	0.85
7 x 7 plot grid	< ~7m	*S. arvensis*	75	69	1.11	0.36
		B. arvensis	72	66	1.67	0.15
		P. rhoeas	76	70	0.12	0.99
		C. cyanus	57	51	0.86	0.51
		N. arvensis	51	45	0.73	0.60
Study site, edge or interior plot	–	*S. arvensis*	75	69	1.31	0.27
		B. arvensis	72	66	1.98	0.09
		P. rhoeas	76	70	0.23	0.95
		C. cyanus	57	51	0.21	0.96
		N. arvensis	51	45	0.47	0.79

Two-sided analysis of variance (ANOVA) tests with background competitor species as a fixed effect (with d.f.=5) show that pollen limitation (quantified by the log-ratio of per germinant seed production under ambient pollination over per germinant seed production with pollen supplementation) differed significantly as a function of the identity of the competitor species within the same plot as the focal individuals for all species except for self-compatible *B. arvensis*. This "within-plot" effect indicates that plant neighbors within a plot affected the pollen limitation of focal plants. However, plants in neighboring plots may also attract pollinators away from focal individuals, effectively competing for pollinators at larger spatial scales. Moreover, the background species in the array of neighbouring plots differed between individual plots due to the random assignment of competitor identity to plot. Multiple linear regression analyses with the number of surrounding plots with each background species as predictor variables (two-sided; each with 1 d.f.), however, showed that pollen limitation was not significantly affected by the identity of the competitors for pollinators at any spatial scale in our study larger than the focal plot (i.e., within an *n* x *n* plot grid centered on the focal plot, where *n*=3, 5, 7). In addition, two-sided ANOVA tests show that pollen limitation was not significantly affected by whether focal plants were in plots at the edge or interior of our plot array (a fixed effect with d.f. =1), suggesting that pollinators were not, for example, favoring plants in plots nearest to the surrounding matrix. Together, these analyses suggest that while pollinators must be making foraging decisions at larger spatial scales than those of our plots, pollinator decisions about which plants to visit within a plot most strongly determined plant performance.

Extended Data Table 4 | Effects of pairwise competition for pollinators in all possible three-, four-, and five-species communities

		Triplets										**Quadruplets**					**Five**
		S, B, P	*S, B, C*	*S, B, N*	*S, P, C*	*S, P, N*	*S, C, N*	*B, P, C*	*B, P, N*	*B, C, N*	*P, C, N*	*S, B, P, C*	*S, B, P, N*	*S, B, C, N*	*S, P, C, N*	*B, P, C, N*	All
Without competition for pollinators	Niche difference, Ω	0.105	0.043	0.05	0.035	0.06	0.29	0.025	0.06	0.05	0.27	0.01	0.005	0.02	0.05	0.02	0.003
	Fitness difference, θ	39.8	45.2	60.8	40.2	46.9	62.8	14.3	45.3	72.1	43.2	45.6	54.9	68.5	55.8	52.2	61.3
	Interaction outcome	*S*	*S*	*S*	*S*	*S*	*S*	*B, P, C*	*B, P*	*B, C*	*P, C*	*S*	*S*	*S*	*S*	*B, P, C*	*S*
With competition for pollinators	Niche difference, Ω	0.004	0.005	0.02	0.003	0	0.02	0.024	0.05	0.02	0.01	0	0.001	0	0	0.01	0
	Fitness difference, θ	15.2	14.0	29.6	12.1	18.3	21.0	4.4	54.6	66.5	51.4	17.0	28.0	30.2	22.4	51.2	29.4
	Interaction outcome	*S*	*S*	*S*	*S*	*S*	*S*	*C*	*P*	*C*	*C*	*S*	*S*	*S*	*S*	*C*	*S*
Change in niche difference		-0.10	-0.04	-0.03	-0.03	-0.06	-0.27	-0.001	-0.01	-0.03	-0.26	-0.01	-0.004	-0.02	-0.05	-0.01	-0.003
Change in fitness difference (degrees)		-24.6	-31.2	-31.2	-28.1	-28.6	-41.8	-9.9	9.3	-5.6	8.2	-28.6	-26.9	-38.3	-33.4	-11.0	-31.9

Effects of competition for pollinators on the structural analogs of the niche difference, Ω, and average fitness difference, θ, using a structural stability approach to coexistence[26] (Supplementary Methods). Interaction outcomes were evaluated by simulation; letters indicate species that persisted in the model (S = *S. arvensis*; B = *B. arvensis*; P = *P. rhoeas*; C = *C. cyanus*; N = *N. arvensis*). Direct comparison between the magnitudes of the structural analogs of the niche and fitness differences are not possible with these particular metrics[26].

nature research

Corresponding author(s): Christopher A. Johnson

Last updated by author(s): Apr 12, 2022

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
☒	☐	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. F, t, r) with confidence intervals, effect sizes, degrees of freedom and P value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's d, Pearson's r), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Microsoft Excel (v. 16.48).
Data analysis	R (v. 3.6.3) and Mathematica (v. 12.0). Zenodo:

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

Data and codes are available on Zenodo:

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We parameterized mathematical models with field data on plant per germinant fecundity as a function of the number of germinated neighbors within a 20-cm radius for all pairs of 5 annual plant species. Focal individuals of each plant species competed against a single background competitor within each plot, which varied in the identity and density of the competitor species. Two focal plants per species per plot were randomly assigned to two treatments: supplemental hand pollination and a control treatment in which plants received only natural pollination. Hereafter, we refer to this experiment as the "competition experiment". A separate experiment simulated pollinator decline by enclosing replicate plots sown with all five plant species under one of two treatments: a pollinator decline treatment, in which only a single pollinator species (male Bombus terrestris) was maintained, and a control treatment in which the communities were accessible to the ambient pollinator community. Hereafter, we refer to this experiment as the "pollinator decline experiment".
Research sample	We selected five common annual plant species commonly found in field margins in dry, hilly, calcareous soil regions of Switzerland. The five species were sown across one hundred and two 2.25-m2 plots. The number of plant species and replicates were determined by the number of available plots. The species are Sinapis arvensis (Brassicaceae), Buglossoides arvensis (Boraginaceae), Papaver rhoeas (Papaveraceae), Centaurea cyanus (Asteraceae), and Nigella arvensis (Ranunculaceae). Seeds for the experiment were collected from species' natural habitats in the field and propagated at the field site. All species are annual and hermaphroditic. We manipulated the plants by hand pollinating a subset of the focal individuals. Individuals in the control treatment were marked in the same manner, but did not receive hand pollination. The sample was meant to represtent a small meadow of annual plants.
Sampling strategy	In the competition experiment, we sampled all focal individuals in each of the experimental plots. The sample sizes were determined by the number of available plots, with 10 focal individuals per plot. We estimated per capita seed production by counting the number of fruits produced by each focal individual and then multiplying by the average number of viable seeds per fruit. Because it was not feasible to count the total number of seeds produced by each focal individual, we did so for ten S. arvensis siliques per individual, all collected nutlets of B. arvensis, and three fruits per individual of P. rhoeas, C. cyanus, and N. arvensis. In the pollinator decline experiment, we quantified the number of plants per plot by counting the number of individuals within four 40-cm diameter circular subsamples (~22.5% of the plot area) and then multiplying by 1/0.225 to get the plot level estimate. We estimated the average seed production per plot by counting the number of fruits produced by 8 haphazardly-selected individuals per species per plot and then multiplying the fruit number by the average number of seeds per fruit. Because it was not feasible to count the total number of seeds produced by each plant, we did so for ten S. arvensis siliques per individual, ten nutlets per individual of B. arvensis, and three fruits per individual of P. rhoeas, C. cyanus, and N. arvensis per plot. These sample sizes were sufficient to statistically estimate all parameters in the population model for the competition experiment and perform a least-squares linear regression of the log-ratios of the per capita population growth rate and floral visitation under pollinator decline relative to with the ambient pollinator community.
Data collection	Data on the number of fruits produced per individual was collected in the field. In the fall, the average number of viable seeds per fruit was estimated in the laboratory. C.A. Johnson, P. Dutt, M. von Rütte, A. Bieger, C. Hess, M. Negreiros, A. Reid, and R. Zäch collected data. Floral visits were recorded in the pollinator decline experiment by P. Dutt using a handheld digital voice recorder.
Timing and spatial scale	The experiment was performed during the growing season of the annual plant species from May to September, 2018. Hand pollination was performed at least twice per week during the season, which was the most frequent that we were able to hand pollinate all of the focal individuals in the experiment. One hundred and two 2.25-m^2 plots were arranged within a roughly 650-m^2 area mimicking a small, patchy meadow. The spatial scale was determined by the plot placement at the experimental study site. We measured each focal individual's per capita seed production as a function of the number of germinated neighbors that it faced within a 20-cm radius, which is a standard spatial scale for annual plant competition experiments.
Data exclusions	No data were excluded from the analyses.
Reproducibility	No attempts were made to repeat the experiment because replicates were built into the experimental design and the experiment was too large in scope to be readily repeated in subsequent years.
Randomization	Background competitor species were randomly assigned to the plots, insuring only that the same species was not sown in directly-neighboring plots to minimize highly-clumped floral displays across plots. Pollination treatments were randomly assigned to focal individuals in each plot. In the pollinator decline experiment, plots were randomly assigned to treatment.
Blinding	Blinding was not possible because the experimenters were hand pollinating individuals.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Precipitation totaled 624 mm over the course of the experiment. Average daily temperature between May and August at 5-cm above the soil was 19.7 C.
Location	The experiment was conducted at the Eschikon-Lindau Field Station of the ETH Zürich, Switzerland (47.449°N, 8.682°E), 556 m above sea level.
Access & import/export	We did not access natural habitats for the experiment. Rather, we used previously-established plots at an agricultural field station.
Disturbance	No disturbance was caused because the experiment was conducted in previously-established plots at an agricultural field station.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology and archaeology
☒	☐	Animals and other organisms
☒	☐	Human research participants
☒	☐	Clinical data
☒	☐	Dual use research of concern

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging