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Negative impacts of dominance on bee communities: Does the influence of invasive honey bees differ from native bees?

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Abstract. Invasive species can reach high abundances and dominate native environments. One of the most impressive examples of ecological invasions is the spread of the African subspecies of the honey bee throughout the Americas, starting from its introduction in a single locality in Brazil. The invasive honey bee is expected to more negatively impact bee community abundance and diversity than native dominant species, but this has not been tested previously. We developed a comprehensive and systematic bee sampling scheme, using a protocol deploying 11,520 pan traps across regions and crops for three years in Brazil. We found that invasive honey bees are now the single most dominant bee species. Such dominance has not only negative consequences for abundance and species richness of native bees but also for overall bee abundance (i.e., strong “numerical” effects of honey bees). Contrary to expectations, honey bees did not have stronger negative impacts than other native bees achieving similar levels of dominance (i.e., lack of negative “identity” effects of honey bees). These effects were markedly consistent across crop species, seasons and years, and were independent from land-use effects. Dominance could be a proxy of bee community degradation and more generally of the severity of ecological invasions.

Key words: *Apis mellifera*; dominance; exotic species; invasion; pollinators.

INTRODUCTION

Small numbers of species typically dominate communities, and they often have outsized impacts on the communities they inhabit (Smith and Knapp 2003, Sasaki and Lauenroth 2011, Czarnecka-Wiera et al. 2019). Invasive species are notorious for their ability to reach high abundances and dominate native environments (Goulson 2003, Torchin et al. 2003, David et al. 2017). Dominant invasive species may outcompete native species and monopolize resources, and they can even transmit novel diseases or act as pests (Crowl et al. 2008). The kudzu vine (*Pueraria montana* (Lour.) Merr.; Fabaceae), for instance, can blanket virtually entire habitats, severely limiting opportunities for and outright killing native competitors (Forseth and Innis 2004), and domestic cats (*Felis catus* Linnaeus, 1758; Carnivora, Felidae) are implicated in the death of astronomical numbers of native species, even causing their extinction (Woinarski et al. 2017, Li et al. 2021). Despite the critical role of dominant species, whether the influence of dominance by invasive species on community abundance and richness is greater than the influence of dominance by native species, remains largely unexplored.

The western honey bee subspecies (*Apis mellifera* Linnaeus, 1758) was originally introduced to Brazil in the mid-19th century for honey production. To improve productivity in tropical areas, an African subspecies (*Apis mellifera scutellata* Lepeletier, 1836) was imported in 1956 (Moritz et al. 2005). Following their quick (1957) escape from containment, these African honey bees have now spread throughout much of South America and even into the southern United States, being considered one of the most rapid and extended biological invasions known (Moritz et al. 2005). Since the African honey

bee’s range expansion, there have been controversies regarding its impact on the native flora and bee species, ranging from potentially positive effects (such as the enhancement of the stability of plant-pollinator networks; Aizen et al. 2008) or small negative effects (Moritz et al. 2005) to large negative effects (Geldmann and González-Varo 2018, Valido et al. 2019, Herrera 2020). Honey bees are thought to negatively affect native bees through competition, changes in plant communities, or transmission of pathogens (Mallinger et al. 2017), but it remains unknown how the dominance by this invasive species impacts bee abundance or species richness in comparison with other dominant native bees (Giannini et al. 2015), and whether such effects may be moderated by access to native habitat.

Here, we quantify the degree to which single-species dominance, the identity of the dominant species (invasive honey bees or native species), isolation from natural and seminatural areas, pan-trap placement within or outside crop, and crop blooming status, and their interactions, influence total bee abundance, native bee abundance, and species richness. We expected bee dominance to reduce bee abundance. This reduction could result from the negative effects of dominant bees on other species described in the previous paragraph and the lack of ability of dominant bees to compensate for the loss of individuals from other species. When invasive species such as African honey bees dominate, they may undermine native bee communities mainly by exploitative competition on floral rewards where native dominant species already occur (Goulson 2003, Mallinger et al. 2017, Herrera 2020), so we expected them to have stronger negative impacts than native dominant species. Therefore, if the competitive ability of honey bees exceeds the ability of native bees, we would expect an

“identity” effect of dominance on bee abundance and species richness rather than a purely “numerical” effect. Alternatively, if both honey bees and native bees exhibit similar competitive ability, the effect of dominance will occur regardless of the identity of the dominant species (invasive vs. native).

METHODS

We tested these ideas through an extensive, standardized protocol deploying 11,520 pan traps across Brazil (Appendix S1: Figs. S1A, S2). We collected and identified 17,831 individual bees across all seasons in seven crops over three years (Appendix S2). Bee sampling followed the protocol in LeBuhn et al. (2016). At each site, one plot with 15 pan traps was deployed within the crop field (at least 10 m away from the edge) and another plot with 15 pan traps in a patch of wild vegetation within 1 km distance from the crop field (Appendix S1: Figs. S3, S4).

The abundance of all bees, the abundance of native bees, and species richness (i.e., the number of species in a community) were modeled through a general linear mixed-effects approach in R (version 3.6.3, *lme4* package, *lmer* function; Bates et al. 2015, R Core Team 2020). Species richness was highly correlated with Shannon (Pearson $r = 0.92$) and Simpson (Pearson $r = 0.82$) diversity indexes across our dataset ($n = 748$); therefore, we present only the results from richness as these do not differ from diversity indices. Fixed effects included dominance (i.e., the proportion of the total abundance accounted by the most abundant species), identity of dominant bee species (native species or honey bees), distance to natural and seminatural areas (\log_{10} meters; Appendix S2 and Appendix S1: Fig. S5), pan-trap placement (inside the crop or in adjacent area), blooming period (crop blooming or not), and their two-way and three-way interactions. For the identity of the dominant bee species, the honey bee category was assigned when the honey bee was the first or second most dominant species. Commonly, when honey bees were the second most dominant species the absolute difference in abundance with the most dominant species was very low so, in this way, we better evaluated the effects of dominance in those environments where the abundance of honey bees is extremely high. We performed the same analyses restricting dominance identity to only first dominant and the conclusions were the same. Our conclusions are also supported by null models (Fig. 2, see details following), which present an independent set of analyses using the strict definition of dominance.

The hierarchical data structure (plots nested within crop species, sampled along seasons and years) was accounted for by including a categorical variable that combined crop species, sampling season and year as a random effect (Fig. 1). This allowed us to estimate different intercepts and slopes of the influences of dominance for each combination of crop species, sampling

season, and year. It also allowed us to account for the fact that, given the different flowering periods of the crops, data for some seasons were absent for some crops. Also, it accounted for the fact that not all crops were sampled during the three years (see Fig. 1 for details). Each season was classified according to the standard procedure for the Southern Hemisphere (summer: 21st December to 21st March; autumn: 21st March to 21st June; winter 21st June to 21st September; spring: 21st September to 21st December). The same analyses were performed for dominance as a response variable to understand the influence of the land-use predictors (Appendix S1: Tables S1, S2). All response variables were \log_{10} -transformed to achieve model assumptions and reduce any potential influence of outliers. No spatial autocorrelation was found in the residuals of the models (*gstat* package, *variogram* function). No corrections (e.g., rarefaction analyses) were necessary for species richness because all plots had the same sampling effort (i.e., 15 pan traps) and we were interested in relative changes in richness across plots (we did not aggregate temporal measures and their dependency was accounted for by the random effects). We tested the Gaussian and homoscedasticity assumptions for the standardized residuals of the models (Zuur et al. 2009) and found that these assumptions were valid.

We performed multimodel inference based on the corrected Akaike’s information criterion (AIC_c) (Harrison et al. 2018). Best-fitting models were selected after evaluating the models resulting from all possible combinations of the predicting variables (dominance, identity of dominance, blooming period, pan-trap placement, and distance to natural and seminatural areas) and their interactions (*MuMIn* package, *dredge* function) (Bartón 2019). Relative importance values (Appendix S1: Table S1) were calculated for each predictor by summing the Akaike weights over all models that include the predictor (*MuMIn* package, *importance* function). The predictor variable with the largest relative importance value is estimated to be the most important for explaining variance in the response variable. We found no clear improvement (lower AIC_c) when considering curvilinear relations, and therefore we present only models with linear form. AIC_c values were obtained from maximum-likelihood estimates of regression coefficients, whereas parameter estimates for final models (i.e., those in Appendix S1: Table S2) were obtained using the restricted maximum-likelihood method (Zuur et al. 2009). Therefore, Appendix S1: Table S1 focuses on the relative importance of predictors, whereas Appendix S1: Table S2 presents the magnitude of effects of these predictors. These are complementary important aspects. We also estimated the marginal r^2 encompassing variance explained by only the fixed effects, and the conditional r^2 comprising variance explained by both fixed and random effects representing the variance explained by the whole model (Nakagawa and Schielzeth 2013), as implemented in the *MuMIn* package (Bartón 2019).

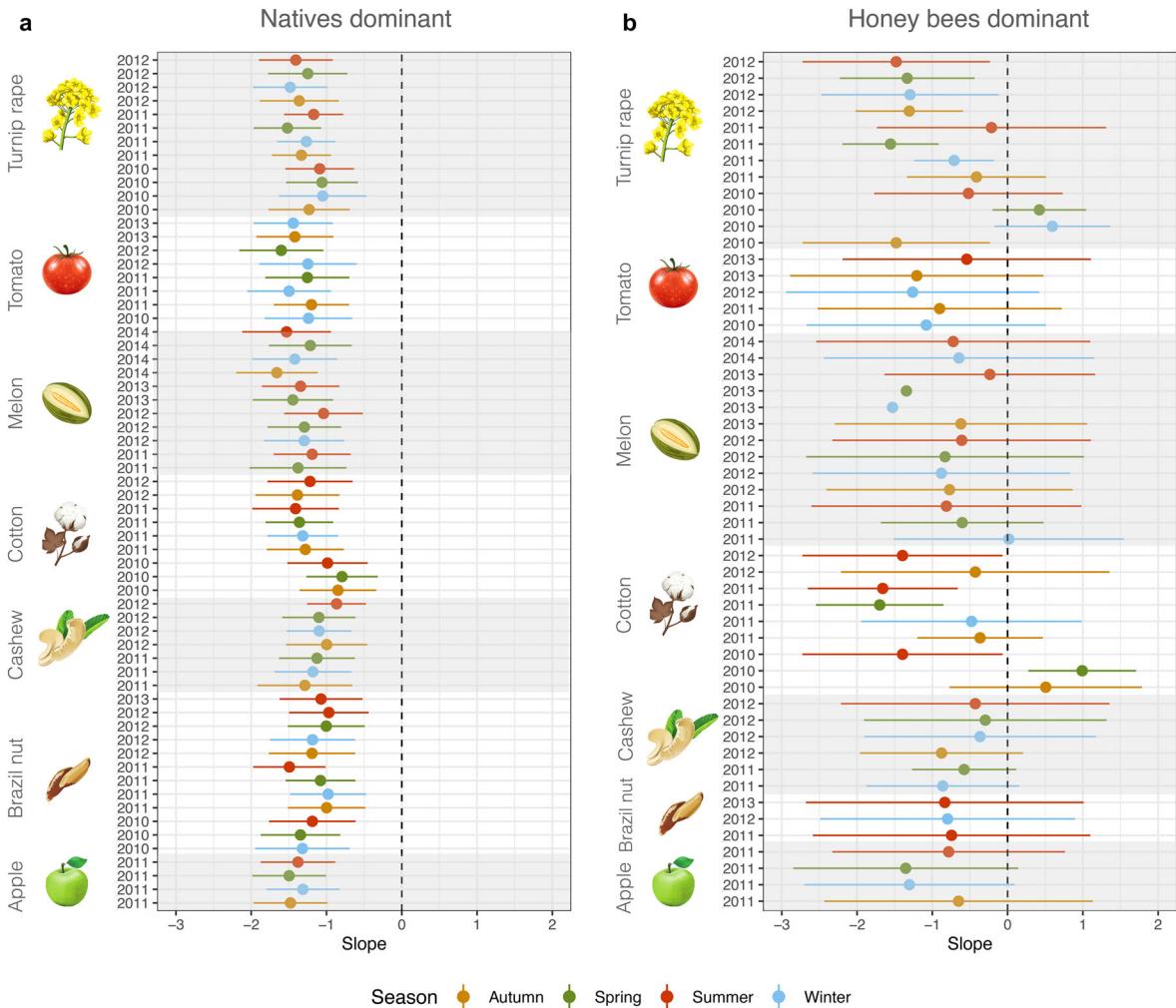


FIG. 1. Slopes for the relationship between total abundance of bees (\log_{10} no. individuals) and dominance (proportion of the total abundance accounted by the most abundant species) for communities in which the honey bee is not the dominant bee (left panel) and those where the honey bee is the first or second most dominant bee (right panel). One slope was estimated for each combination of crop, season, and year.

Finally, we tested whether the observed communities (and species) were more dominant than expected, given their structural constraints. Given some individuals and species, Locey and White (2013) showed the range of expected dominance values. Specifically, species abundance distributions (SAD) are constrained by richness and total abundance, where not all possible SAD forms exist (i.e. only some sets are feasible). This is important, because these feasible sets showed a marked dominance, and produced hollow SAD curves highly correlated with empirical SADs. Then, when comparing across communities with different sizes, it is important to control for community size. To that end, first, we found all possible feasible sets for each community of a particular total abundance (N) and species richness (S), which is equivalent to finding all unordered ways of summing S positive integers to obtain the positive integer N , a combinatorial

approach known as integer partitioning (Locey and White 2013). This generates the expected values of the dominant species for each community. Specifically, for each community with richness values >3 , we randomized 1,000 times (null model) the ways that the abundances of species could sum to a total abundance. Next, we compared this expectation with the observed dominance. In that way, we factored out the role of richness and abundance to assess dominance. To do so, we used a Z-score, resulting from subtracting the observed value to the expected values mean, then dividing by the standard deviation of the expected values. This Z-dominance can be interpreted as how dominant is species X given the constraints imposed by the number of species and the total abundance of the community. Observed Z-values larger than 1.5 standard deviations from the mean expected values denote important differences. Note that

the Z-dominance values of the dominant species were highly correlated with relative abundance ($r = 0.7$).

RESULTS AND DISCUSSION

We found higher bee species richness in Brazilian croplands than previous studies using a different methodology (Garibaldi et al. 2016), reflecting our high sampling effort. Plots located in apple and melon crops hosted the most-diverse bee communities while the least-diverse communities were found in cashew plots (Appendix S1: Fig. S1B). These patterns are likely to reflect differences in crop attractiveness, agricultural practices, and biogeographical characteristics of the regions in which crops are embedded.

Once absent from Brazil, we found that the honey bee is now the most abundant bee overall (Appendix S1: Fig. S1C), in agreement with studies using different methodologies in other locations (Garibaldi et al. 2013, Hung et al. 2018, Herrera 2020). Furthermore, the honey bee (only the African subspecies of honey bee was present in our sampling) was the first or second most dominant bee at 34% of the sites (Appendix S1: Fig. S1D). Honey bees were present in all crop study systems, but with variable abundance: the proportion of total abundance for honey bees ranged from 23% in melon in northeastern Brazil to 1% in Brazil nut in Amazonia (Appendix S1: Table S3). The native *Trigona spinipes* (Fabricius, 1793) was the second most abundant species in Brazil, and the first or second most dominant bee in 7% of the sites, accounting for 48% of all individuals in cotton to nearly 0% in Brazil nut and melon. The honey bee and *T. spinipes* are both eusocial, supergeneralist species (Giannini et al. 2015). Most of the other abundant native bees found in our study, including *Melitoma segmentaria* (Fabricius, 1804), typically build their nests in the soil, often in aggregations (Appendix S1: Fig. S1C, D, Table S3). Interestingly, *T. spinipes* was the only stingless bee detected among the most abundant bee species (Appendix S2), despite their eusocial character and the presence of 243 documented stingless bee species in Brazil (Ascher and Pickering 2020).

Bee dominance was greater in croplands than adjacent habitats, the latter including natural or seminatural habitats in many instances (Appendix S1: Tables S1, S2). This difference between cropland and adjacent habitat was even greater during crop bloom, far from natural and seminatural habitats, and where the honey bee was the first or second most abundant species (see positive interactions in Appendix S1: Table S2). Overall, these results showed that dominance increased with landscape homogenization and conventional agricultural coverage, a pattern consistent with prior research (Garibaldi et al. 2011), suggesting that dominance could be a proxy for habitat degradation.

Despite the association of dominance with land-use variables, it had an independent effect on bee species

abundance and richness. Communities with higher dominance had lower total bee abundance, native bee abundance, and species richness (Appendix S1: Fig. S6). Such effects of dominance were not confounded with the effects of land use: in the models including dominance and the identity of dominant species as predictors (in addition to land-use variables), the r^2 explained by the fixed effects alone increased by factors of 12, 5, and 13 for total abundance, native bee abundance, and species richness, respectively, in comparison with models including only land-use variables as predictors (Appendix S1: Table S2). Indeed, multimodel inference showed that the most important predictors of total abundance, native bee abundance, and species richness were dominance, the identity of the dominant species, the interaction between dominance and the identity of the dominant species, whether pan traps were located inside or adjacent to crops, and bloom status (all the importance values were higher than 0.9; Appendix S1: Table S1). The models with the lowest AIC_c also included these same predictors (Appendix S1: Table S2). The conditional r^2 of the models with the lowest AIC_c for total abundance, native bee abundance, and species richness were 0.65, 0.69, and 0.80 respectively, showing that the model structure explained a high proportion of the total variance considering our widespread sampling effort (Appendix S1: Table S2).

Contrary to expectations (Torchin et al. 2003, Crowl et al. 2008, Mallinger et al. 2017, Herrera 2020, Russo et al. 2021), dominance by honey bees had a smaller negative effect on total abundance and species richness than dominance by native bee species (Fig. 1; Appendix S1: Table S2). Despite high variability among biogeographic regions in Brazil, these results were markedly consistent across crops, seasons, and years (Fig. 1; note that, despite the general trend, we found a diversity of responses for the effects of honey bees that reflected unmeasured variables). When we examined only native bee abundance, there was no influence of the identity of the dominant species on the slope of the relationship between abundance and dominance (Appendix S1: Table S1). This was further supported by a complementary correlation analysis between the abundance of honey bees and native bees (Appendix S1: Fig. S7). Moreover, when randomizing the ways that the abundances of a given set of species can sum to a total abundance (“null models”), honey bees did not show greater dominance than expected in comparison with native bees (Fig. 2). The fact that both the mixed-effects models and the null-model approach showed little to no “identity” effects for the honey bees, suggested that the negative effects of honey bees reported elsewhere (Mallinger et al. 2017, Valido et al. 2019) may be mainly related to a “numerical” (dominance) effect. This means that honey bees do not seem to reduce more native species abundances or species richness than other species that achieve similar, extremely high, levels of dominance. It also implies that the impacts of the honey bee on

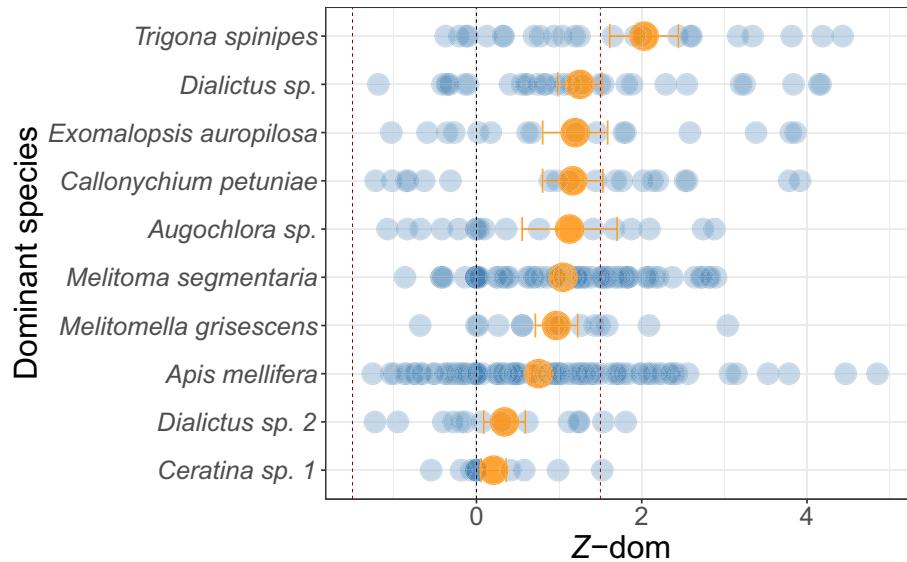


FIG. 2. For each community with richness values >3 , we randomized 1,000 times (null model) the ways that the abundances of species can sum to a total abundance (Locey and White 2013). Then we calculated, for the most abundant species in each community, the difference between the observed and the expected abundance under this null model using Z-values (Z-dom). We show that the most dominant species are not consistently more dominant than expected (values <1.5 SD from the expected values, see dashed lines for 1.5 and -1.5 SD), except for *Trigona spinipes*. Z-dom of the dominant species was highly correlated with its relative abundance (Pearson $r = 0.7$).

ecosystems will be more severe where it is more abundant (Mallinger et al. 2017, Geldmann and González-Varo 2018, Valido et al. 2019).

Our null models showed that *T. spinipes* was the bee species with higher dominance than expected by chance (Fig. 2). *T. spinipes*, the most abundant native bee species, is very aggressive toward other bees, including honey bees (Roubik 1989, Biesmeijer and Slaa 2006). For example, even when floral resources are plentiful, *T. spinipes* chases and attacks honey bees before landing on flowers (Minussi and Alves-dos-Santos 2007). Furthermore, *T. spinipes* foragers competitively exclude *Melipona (Michmelia) rufiventris* (Lepelletier, 1836) foragers from feeders, in some cases even through decapitation (Nieh et al. 2005).

There was no evidence of an interaction between the effects of isolation from natural and seminatural habitats and either dominance or dominant species identity (Appendix S1: Table S1). Interestingly, the effects of dominance on the abundance of native bees were more negative within crops than in adjacent habitats (Appendix S1: Table S2), and are likely to reflect the positive influence of native plant diversity on native bees. As expected (Garibaldi et al. 2011), isolation from natural and seminatural areas decreased the abundance of native bees, while crops hosted lower total bee abundance and species richness than adjacent habitats (Appendix S1: Table S2). In general, total abundance was higher during crop bloom than in the rest of the flowering season, but there was no evidence of an interaction with dominance (Appendix S1: Table S1). Higher

bee abundance is likely to be a consequence of crops usually blooming during the main growing season of each region, and also of higher flower abundance during crop bloom (the latter mechanism is supported by a stronger effect on total bee abundance than on native abundance or species richness; Appendix S1: Table S1). Overall, these results showed an effect of dominance on bee communities that was not confounded with other, previously reported, effects of land-use change (Garibaldi et al. 2011), supporting the generality of our conclusions.

Dominant native species have previously been found to strongly influence community composition, both within and across guilds. For example, the crown of thorns starfish may become exceedingly common and cause coral declines via “outbreaks” enabled by release from predators (Pratchett et al. 2017), and black tailed prairie dogs strongly influence their local plant communities such that their removal or reintroduction can substantially change local flora (Weltzin et al. 1997, Hale et al. 2020). The volume of such studies pale in comparison with the vast literature on dominant invasive species, as a great deal of work is needed to judge such effects on a large scale, suggesting that more work is needed to see how commonly dominant native species might actually play such roles. Even rarer are examples of dominant native species’ impacts on community composition within guilds, although recent research suggests that this may also happen in plants in response to disturbance (Zhao et al. 2021). In our study, it may be that agricultural management in these systems has

sufficiently perturbed local ecosystems such that *T. spinipes* has become exceedingly dominant, however the dominance effects were independent of land-use change variables as stated above.

Our results have implications for understanding the effects of dominance by invasive species, as the negative impact of the African honey bee on native bees can be attributed principally to a quantitative (“numerical”) rather than a qualitative (“identity”) effect. This means that the consequence of the African honey bee invasion on native bee assemblages is basically related to its extremely high abundance, probably associated with its developed sociality, rather than to any intrinsic characteristic associated with its exotic status (Aizen et al. 2020). In any event, increases in dominance by a single species, being the honey bee or any other, can have consequences for wild-plant reproduction and crop yield because of expected decreases in overall pollination efficiency caused by a reduction in pollinator diversity (Garibaldi et al. 2013, 2016). This includes diversity-related pollination effects associated with the likelihood of “sampling” effective pollinators, increase in spatial and temporal niche complementarity, and the occurrence of synergistic interactions between pollinator species (Tscharntke et al. 2005, Fründ et al. 2013). Also, increases in honey bee abundance in isolation can have negative effects on seed set when density-dependent (i.e. numerical) costs of active pollen theft and self-pollination, which are common in plant-pollinator interactions involving this bee species, outpace the benefits of pollen transfer (Aizen et al. 2020). Finally, from an evolutionary perspective, increasing pollinator dominance can involve diminishing opportunities for plant diversification and for adaptive responses to large-scale anthropic disturbances associated with global change (Nuismer et al. 2018).

As the demand for pollinator-dependent crops becomes greater, so does the use of managed bees, therefore increasing its dominance within bee communities (Aizen et al. 2019, Herrera 2020). Here, through a widespread and systematic bee sampling at a continental scale, we found consistent negative effects of bee dominance on species abundance and richness irrespective of crop, season, or year. Furthermore, although a high abundance of honey bees can reduce bee species abundance and richness, this effect seems to be independent of species identity, pointing it out as a general principle that might, in most circumstances, erode different ecosystem processes and services.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.3526/supinfo>

OPEN RESEARCH

Data (Garibaldi et al. 2021) are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qfttd0hm>.