ECOSYSTEM SERVICES

Species turnover promotes the importance of bee diversity for crop pollination at regional scales

Rachael Winfree,[1]* James R. Reilly,[1] Ignasi Bartomeus,[1,2] Daniel P. Cariveau,[1,3] Neal M. Williams,[4] Jason Gibbs[5]

Ecologists have shown through hundreds of experiments that ecological communities with more species produce higher levels of essential ecosystem functions such as biomass production, nutrient cycling, and pollination, but whether this finding holds in nature (that is, in large-scale and unmanipulated systems) is controversial. This knowledge gap is troubling because ecosystem services have been widely adopted as a justification for global biodiversity conservation. Here we show that, to provide crop pollination in natural systems, the number of bee species must increase by at least one order of magnitude compared with that in field experiments. This increase is driven by species turnover and its interaction with functional dominance, mechanisms that emerge only at large scales. Our results show that maintaining ecosystem services in nature requires many species, including relatively rare ones.

We are living in an age of catastrophic species loss but have little understanding of how species loss will affect the delivery of ecosystem services—that is, those ecosystem functions that are essential to human life (*1*, *2*). The role of species richness (i.e., the number of species present in an area) in facilitating ecosystem functions has been a focus of ecological research for decades. Field and laboratory experiments clearly show that many ecosystem functions diminish with declining species richness (*1*, *3*). Whether this observation holds for ecosystem services in natural systems, however, is poorly known (*1*, *4*). The transition from smaller-scale experiments to natural systems has been predicted to both increase (*3*, *5*) and decrease (*6*) the importance of biodiversity to function, and large-scale studies attempted thus far found varying results (*1*, *7*).

For several reasons, species richness may have different effects on ecosystem function in natural landscapes compared with experiments. First, there is the difference in scale: The typical biodiversity–ecosystem functioning experiment covers an area of 3 m^2 (*8*), whereas ecosystem services operate across thousands of square kilometers and therefore include large-scale phenomena such as species distributions and spatial patterns of environmental variation. Second, manipulative experiments control or randomize aspects of community structure other than species richness, whereas natural communities vary not only in richness but also in species composition, relative abundance of each species (dominance), and the total number of individuals (abundance). Variation in these factors, as well as natural environmental variation, could modify or overwhelm the importance of species richness to ecosystem services. Third, the mechanisms that drive the biodiversity-functioning relationship in experiments operate at the within-community scale and are based on interactions among species or differences in their functional traits (*3*, *8*). By contrast, in natural landscapes the among-community scale is also relevant and will likely be governed by different mechanisms (*9*). The different questions investigated by biodiversity–ecosystem function research at the experimental versus the landscape scale are portrayed in Fig. 1, A and B.

Two well-known aspects of species' distributions lead to opposing predictions about how many species are needed to sustain ecosystem services at large scales. First, species turnover, or beta diversity [in its broad sense of changes in species identity and abundance across ecological communities (*10*)], should cause the number of species needed to increase with increasing spatial scale (*3*, *8*, *11*). Specifically, because different species are needed to provide the same function in different places, the cumulative number of species required is predicted to increase monotonically with increasing scale, analogous to the species-area relationship (*3*). The second, and contrasting, prediction stems from the fact that all natural ecological communities have high numerical dominance, with a few abundant species and many rare ones (*12*). Evidence suggests that the numerically dominant species provide most of the ecosystem services as well (*13*, *14*), raising the possibility that in nature ecosystem services might be provided by a small number of functionally dominant species.

We measured the number of species needed to provide a target level of ecosystem services as the number of sites at which the target must be met increases. We studied crop pollination by wild (unmanaged) bees, a globally important ecosystem service (*15*), at 48 commercial crop fields (hereafter "sites") in the Mid-Atlantic region of the United States. Parallel study designs and methods were used for each of three crop systems (watermelon, blueberry, and cranberry) (Fig. 1C). Within each site, we net-collected bee pollinators visiting crop flowers within a 50- to 200-m^2 transect, an area on par with that of many biodiversity-function experiments. Our sites were distributed throughout an ~3700-km^2 area, such that the spatial scale of our analysis, as it increased from 1 to 48 sites, varied across five orders of magnitude. We also measured the pollination provided by each type of bee by counting pollen grains deposited on experimental flowers. We then found the minimum set of bee species that could meet various pollination thresholds (25, 50, and 75% of the observed mean) at each site in a set of 1:48 sites (*16*). We plotted the cumulative number of bee species needed against the number of sites, as in Fig. 1B. To estimate the effect of dominance, we compared our observations with the results of a null model that removed dominance.

Our findings provide empirical support for the often proposed but rarely tested hypothesis that ecological research has underestimated the importance of biodiversity to ecosystem services in nature. At our smallest spatial scale, achieving the 50% pollination threshold required 5.5 bee species (95% confidence interval: 4.5 to 6.6 species). This is on par with findings from biodiversity-function experiments, which have indicated that fruit and seed set reach an asymptote with pollination by only three to five bee species (*17*, *18*). As spatial extent expanded from the site to the landscape (16 sites arrayed across hundreds of square kilometers) (Fig. 1C), however, the number of bee species required to achieve the 50% threshold level of pollination increased by a factor of 4.4 (mean; range: 3.9 to 4.7) (Fig. 1D). When all three crop systems were considered together, achieving the 50% threshold at 48 sites required 55 bee species, and achieving a 75% threshold required 79 species, or most of the bee species we observed (Fig. 1D and fig. S1). Lastly, although with only three crop systems we cannot make any inferences about the spatial scale at which all of the important pollinator species are known, in two of our three systems the species accumulation curves do not reach an asymptote. This suggests that considering additional sites would reveal even more species to be important (Fig. 1D).

The patterns we observed result from the combined effects of species turnover and dominance, which act simultaneously and are difficult to disentangle (*10*). We solved this problem by developing a graphical model that partitions the increases in species required into these two effects (Fig. 2A). We used a null model (Fig. 2, A and B,

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[1]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA. [2]Doñana Biological Station–Consejo Superior de Investigaciones Científicas, Seville, Spain. [3]Department of Entomology, University of Minnesota, St. Paul, MN, USA. [4]Department of Entomology and Nematology, University of California, Davis, Davis, CA, USA. [5]Department of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada.
*Corresponding author. Email: rwinfree.rutgers@gmail.com

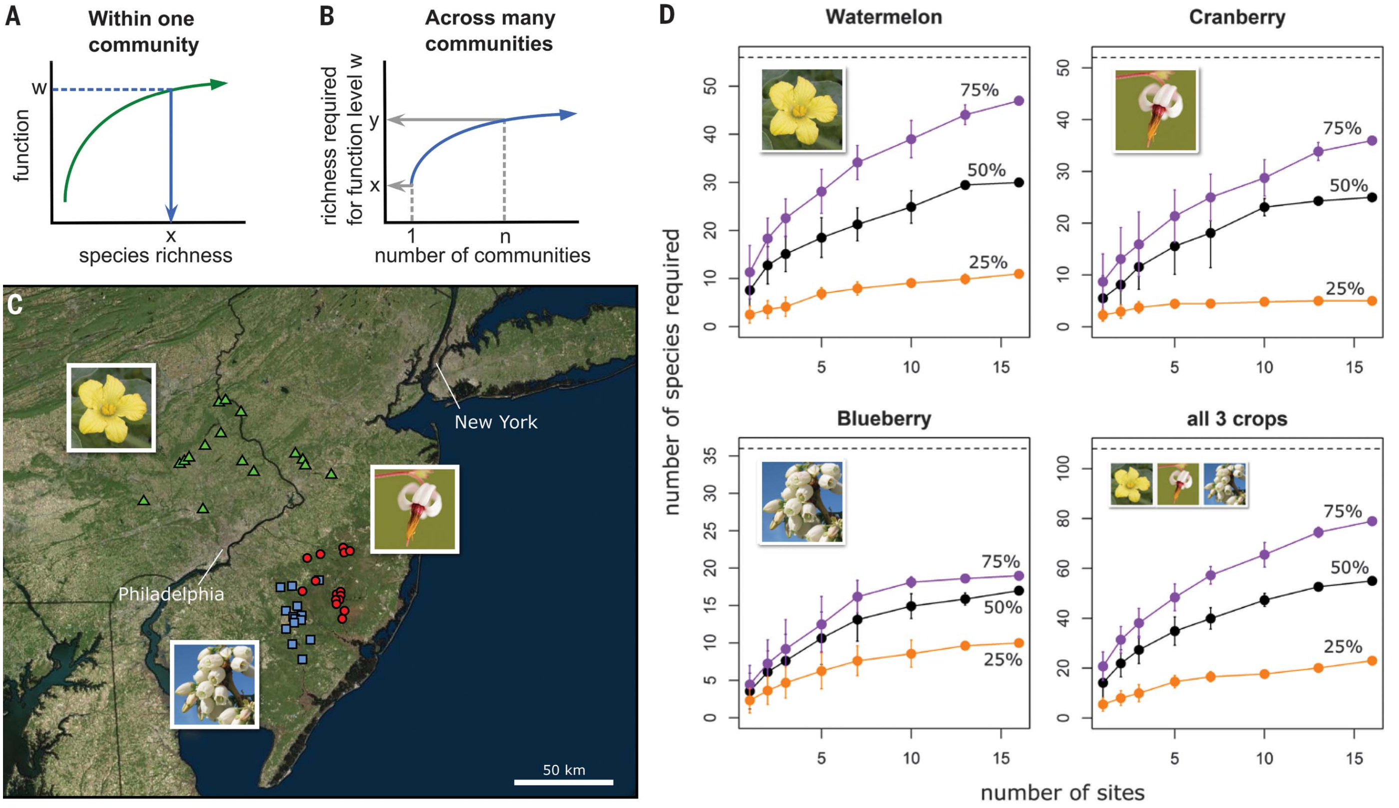

Fig. 1. How the number of bee species needed to provide pollination changes with increasing spatial extent. (**A**) A typical graph from a biodiversity-function experiment shows that a certain number of species (*x*) is needed to achieve a given level of function (*w*) within one community. (**B**) By contrast, studying ecosystem services at large scales requires analyses across communities. The threshold level of function *w* is now implicit, and the cumulative number of species required to achieve function level *w* at all *n* communities is plotted as a function of increasing spatial extent. In this example, *x* species are needed to provide function level *w* in one community, and *y* species are needed to provide function level *w* in each of *n* communities across an entire landscape. (**C**) Commercial crop fields of watermelon (green triangles), cranberry (red circles), and blueberry (blue squares) in New Jersey and Pennsylvania, USA, where bee biodiversity and crop pollination were measured. (**D**) Cumulative number of bee species required to maintain thresholds of 25% (orange), 50% (black), and 75% (purple) of the mean observed level of pollination, at each of *n* sites (*16*). Horizontal dashed lines indicate the total number of bee species observed in each study. Error bars represent 1 SD over all possible starting sites for expanding the spatial extent. For all three crops combined, each *x*-axis increment represents the addition of one site per crop.

red line) to remove dominance from the data by redistributing the total pollination delivered to each site equally among all of the bee species at the site while maintaining the observed species richness, species identity, and total pollination at each site. This approach removes the effects of dominance across communities [i.e., the larger-scale effect of dominance that arises because locally abundant species also tend to be widespread (*19*)] as well as within communities, because when no species are dominant within sites, dominant species cannot be shared across sites. Results of this null model show how many species would have been required to meet the pollen delivery threshold in the absence of dominance. Graphically, the difference between the null model and our observations is the effect of dominance (Fig. 2B, green arrows), whereas the difference between the first and *n*th site is the effect of species turnover (Fig. 2B, blue arrows).

Without dominance, more bee species would have been needed to meet the pollination threshold, which is not surprising given that functional dominance was strong in all three study systems (fig. S2). However, turnover had stronger effects than dominance at most spatial scales, and the relative strength of turnover increased with the scale of analysis (Fig. 2C). At the largest spatial extent, the number of species added because of turnover effects was 14 times (mean; range: 0.3 to 58.2) the number subtracted from it because of dominance (compare green and blue arrows in Fig. 2C and figs. S3 and S4). How the effect of dominance might change with scale, and the relative magnitude of the effects of dominance and turnover, was not previously known for any ecosystem service. Our finding that, even when present, strong functional dominance has relatively weak effects on the number of species needed does not support the hypothesis that dominance typical of natural communities will necessarily limit the importance of diversity in nature (*6*, *20*–*22*).

Previously, the effect of spatial scale on biodiversity-function relationships has been explored by aggregating experiments (*11*) but without investigation of species turnover and dominance. Most experimental communities are artificially assembled by researchers, which precludes measuring turnover in a meaningful way because any turnover observed would result from the researchers' decisions about what species to use in their experimental communities. Likewise, most experiments have excluded dominance as part of the experimental design at the within-community (plot) scale and have randomized species composition across plots, which prevents larger-scale dominance from occurring (*23*). By contrast, previous work done at large spatial scales in natural systems has shown that ecosystem services rely heavily on a few dominant species (*14*, *20*, *21*, *24*). These studies have combined data across many sites or an entire region (e.g., Amazonia) and found that a small proportion of species (often <5%) provides 50% or more of the ecosystem services (*14*, *20*, *24*). Similarly, in our own previous work, we concluded that a few dominant species were important because they explained a large proportion of the variation in pollination between sites (*21*).

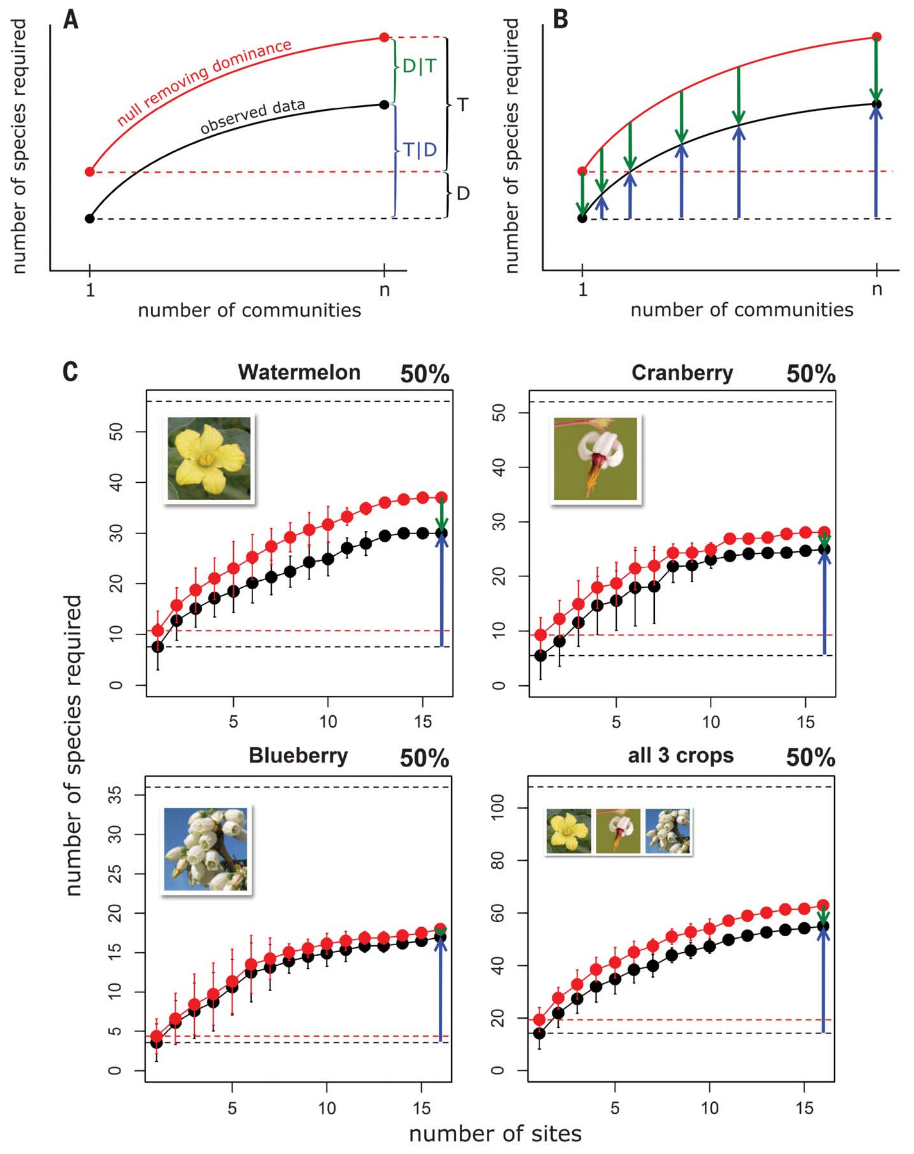

Fig. 2. How species turnover and dominance determine the number of species required for ecosystem services. (**A**) Conceptual diagram showing how observations (black; as in Fig. 1D) could be compared with a null model (red) that assumes each species in a community contributes the same amount of ecosystem services. D represents the effect of dominance in the absence of turnover (i.e., at only one site). T denotes the effect of turnover in the absence of dominance. T|D represents the effect of turnover in the presence of dominance, thus matching data as observed in the field. D|T is the effect of dominance in the presence of turnover (i.e., the number of additional species that would be needed in the absence of dominance). (**B**) Same as (A), but showing how the relative contribution of T|D increases with increasing spatial scale (blue arrows), whereas that of D|T may not (green arrows). (**C**) Observed data from this study (black) plotted against the null model (red), as in (A). Green and blue arrows are as in (B); horizontal dashed lines are conceptually the same as those in (A) and (B) (i.e., the lines show baseline values at number of sites = 1). Data were plotted for the 50% threshold.

In this study, we took a different approach based on an absolute rather than proportional measure, and we found many species to be important. We believe that the difference arises from contrasting approaches to scaling up biodiversity–ecosystem function research from experiments to nature, for which there is currently no accepted method (*2*). Our approach requires that a fixed threshold level of pollination be provided at all sites as the number of sites increases. Unlike the proportional approaches described above, a threshold approach is sensitive to species turnover not only of the dominant species but also of less abundant species that may be important contributors to pollination at a single site or year (*25*). It is also sensitive to variation across sites in the total amount of pollination received, such that sites with low levels of pollination will require most or all of their species, including the rare ones, to reach the threshold (fig. S5). Lastly, our method aligns with the human perspective on ecosystem services, because each farmer requires his or her crops to be adequately pollinated. We believe this is the conceptual approach that best corresponds to the goal of scaling up biodiversity–ecosystem functioning research from experiments to nature, and it shows that as area increases, most species are found to be important.

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SUPPLEMENTARY MATERIALS

www.sciencemag.org/content/359/6377/791/suppl/DC1
Materials and Methods
Figs. S1 to S5
Tables S1 and S2
References (*26*–*39*)

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Many, many more pollinators needed

Numerous studies have shown that biodiversity is necessary for ecosystem function. The majority of these, however, have taken place at relatively small experimental scales. Winfree *et al.* looked across more than 3000 square kilometers for relationships between biodiversity and crop pollination (see the Perspective by Kremen). The number of wild bee species required for successful pollination rapidly increased with spatial scale, largely owing to variation in the species present across sites and the degree to which the most abundant species played a role. In the end, more than an order of magnitude more species than predicted by smaller-scale experiments were required for full ecosystem functioning.

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