

BIODIVERSITY

Common competitors and rare friends

Data from hundreds of natural communities show that rare species share more positive associations with each other than abundant species, which tend to be more segregated. These patterns are consistent with facilitation for rare species and competition for abundant ones, and hold true across taxa and biogeographic regions.

Jes Hines and Petr Keil

Biological diversity is distributed unequally across the globe. To identify biodiversity patterns and explain the processes that generate them, some scientists use species-distribution modelling to describe how each species has a unique distribution. Others, however, emphasize that species organize themselves in recurrent community patterns seen again and again in different contexts. For example, community ecologists have observed a ubiquitous pattern across ecosystems whereby many species are rare, and a few species are common. But why do rare species persist? And what limits the distribution of common ones? Discovering the answers to these questions may depend on uniting species-distribution and community-based approaches. Writing in this issue of *Nature Ecology & Evolution*, Calatayud et al.¹ take a significant step toward doing so, and toward answering these questions, by revealing a novel and pervasive ecological pattern. That is, rare species tend to form positive

associations with each other, while the opposite is true for common species.

Compiling community assemblage data from a wide variety of plant and animal taxa found in many biomes around the world, Calatayud et al. used community abundance patterns to establish association matrices for networks of co-occurring species (Fig. 1). Next, they decomposed their data into positive and negative spatial associations, and evaluated whether observed patterns were more, or less, common than could be generated by chance (Fig. 1). Across more than 90% of the data sets, they discover that negative associations among species (repulsions) are more common than positive associations (aggregations). Moreover, when positive associations occur, they were typically among rare species that were associated with particular sets of other rare species. That is, rare species tended to occur in more modular network patterns than abundant species. The authors speculate that competition is likely to be a

primary mechanism driving repulsions and limiting dominance of common species, whereas facilitation underlies the positive associations supporting persistence of rare species¹.

The idea that co-occurrence data hold information useful for understanding assembly of ecological communities has been the source of a long and contentious debate. Stephen Alfred Forbes was one of the first to use semi-quantitative analysis to document association patterns in fish assemblages as far back as the early twentieth century². By the 1920s, however, Ellis Michael had already critiqued association-based approaches, pointing out that the outcome of analyses would depend on spatial scale of sampling if environmental conditions were heterogeneous³. Debate became re-ignited following prominent research on co-occurrences by Jared Diamond in the 1970s, who proposed that competition should lead to predictable patterns of segregations in ecological

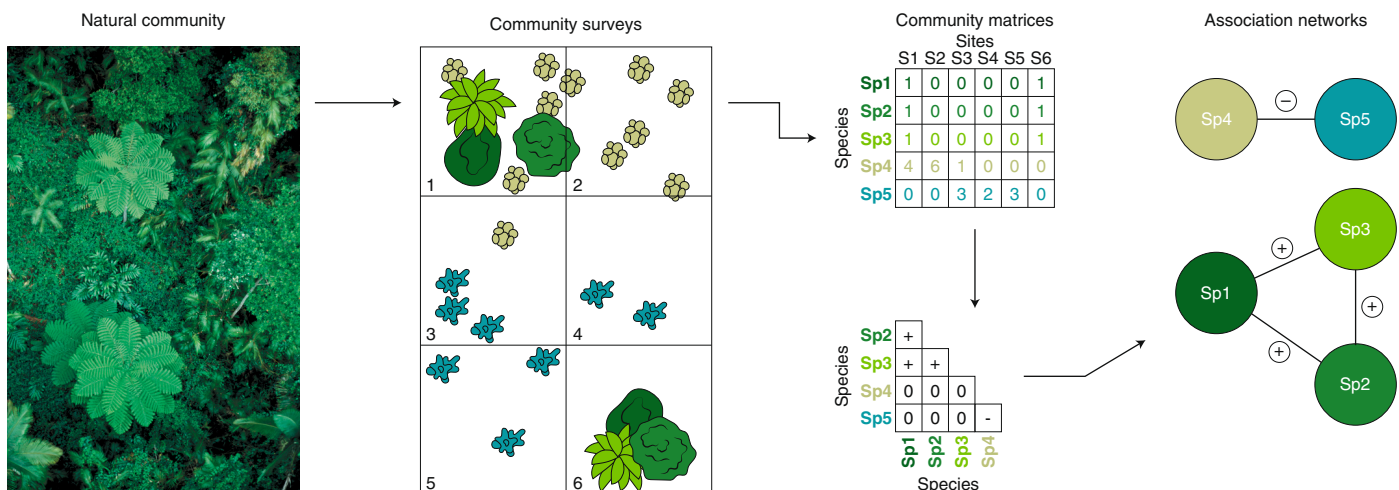


Fig. 1 | Common and rare species occur in distinct patterns of negative and positive associations, respectively. Using community matrix data from surveys of more than 300 natural communities around the world, Calatayud et al. discover a new biodiversity pattern. Rare species (for example, species 1, 2 and 3, which occur in only two of the sites and in low abundance) tend to have more positive associations by co-occurring together at the same sites. In contrast, common species (for example, species 4 and 5, which occur in three of the sites and in higher abundance) have more negative associations in the species co-occurrence network. Photo credit: CSIRO.

communities⁴. For many years, researchers argued about whether segregation stemmed from competition or whether patterns were influenced simultaneously by other factors such as environmental niches, dispersal limitation or trophic interactions. To maximize the possibility that the co-occurrence patterns observed by Calatayud et al. were the result of non-trophic biotic interactions, they gathered data from species feeding at the same trophic level that were found in relatively homogenous habitats at small spatial extents¹. To this day, however, critiques of co-occurrence networks highlight disadvantages of association patterns, particularly with respect to using them to infer underlying mechanisms^{5,6}, even though species co-occurrences can show intriguing patterns over broad spatial and temporal scales^{7,8}. Therefore, it is refreshing to see that Calatayud et al. use several simulations to test how well the patterns they find can be reproduced by other mechanisms¹. Their simulations lend some credence to the suggestion that common species compete, while rare species retreat to pockets of microhabitats, which is a new and testable modification of Diamond's original hypothesis.

A clear next step is to support the results of Calatayud et al. with experimental tests of the causes and consequences of the different association patterns they identify. For example, a major impetus for monitoring and conserving biodiversity has been based on concern that diversity loss has implications for ecosystem functioning. Nearly 30 years of research has demonstrated that diversity drives temporal and spatial stability of fundamental ecosystem processes. Yet, many experiments designed to test relationships between biodiversity and ecosystem functioning

do not use natural communities, leading to persistent criticism that experiments do not accurately capture the ecosystem consequences of real species associations or realistic biodiversity change^{9,10}.

The real-world patterns revealed by Calatayud et al. open a new line of inquiry about how mechanisms that promote co-existence of rare and common species may contribute to biodiversity effects on ecosystem functioning. On the one hand, rare species tend to be functionally unique, and one could speculate that positive associations among functionally unique species may enhance ecosystem functioning. By nature, however, rare species may contribute little overall to key ecosystem functions, like production of biomass. Either way, it is likely that including spatially explicit data on microhabitat structure within assemblages can shed light on whether, and how, rare species aggregate, and how much facilitation contributes to their influence on ecosystem functioning¹¹. The patterns revealed by Calatayud et al. make it increasingly clear that realistic tests of diversity–function relationships should be combined with manipulations of community abundance, community assembly mechanisms and species spatial associations.

Even though Calatayud et al. do not directly address the problem of how to infer biotic interactions from observed co-occurrences, they reveal a pronounced and consistent biodiversity pattern. In doing so, they strengthen the connection between species distribution modelling and community abundance patterns, demonstrating that, in the future, commonness and rarity may be important predictive components of joint species distribution models¹². Notably, they exclude from their analysis assemblages with fewer

than ten species, and so whether patterns hold in species with poor assemblages remains an open question¹. Nonetheless, one of the most impressive features of the authors' data is the consistent pattern detected across the global distribution of ecological communities. Discovery of similarly consistent patterns, such as the systematic increase of biodiversity towards the tropics and species area relationships, have had major implications for conservation of biodiversity and estimation of anthropogenic species loss. Therefore, regardless of whether Calatayud et al. unequivocally demonstrated mechanisms underlying their results, the patterns will inspire exciting prospects for future biodiversity research. □

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Competing interests

The authors declare no competing interests.