

ECOLOGY

Diversity breeds complementarity

Evolutionary and ecosystem processes have long been treated as distinct. The finding that interactions among plant species cause rapid evolutionary changes that affect ecosystem function suggests that it is time for unification.

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The great naturalist Charles Darwin proposed his theory of evolution by natural selection as a unifying explanation for patterns seen in the natural world. But the unity sought by naturalists gave way to more-fragmented perspectives as natural history itself speciated into the modern disciplines of ecosystem ecology, community ecology, population biology, palaeontology and evolution. In a paper published on *Nature's* website today, Zuppingger-Dingley and collaborators¹ have taken a significant step towards a reunification of these disciplines. Their findings in an experimental study of plants suggest that ecosystem and evolutionary processes cannot be separated: ecological interactions among a large number of plant species can cause rapid evolutionary changes that, in turn, influence ecosystem processes.

An idea central to both ecology and evolution is that of the niche — the set of environmental conditions in which a particular species thrives. In ecology, niche differences among species help to explain why large numbers of competing species coexist, and why greater plant diversity leads to greater ecosystem productivity². In evolutionary biology, the niche concept features prominently in our understanding of how new species arise. Competition between closely related species drives the evolution of trait differentiation, such as bird beaks that are specialized for different seeds or lizard limbs that are suited for either climbing or walking. The evolution of such character displacement can be seen in laboratory experiments using microorganisms³ and in field studies of incipient species formation, such as in Darwin's finches on the Galapagos Islands⁴.

In their study of character displacement, Zuppingger-Dingley and collaborators made use of experimental field plots in which 16 species of grassland plant were grown either in monocultures or in mixed plots of 4 or more species for 8 years. They then collected these plants, propagated them in the lab, and

assembled the offspring in new communities: either monocultures or mixed communities of two species. They observed that, relative to the monocultures, the 8-year period of selection in the high-diversity communities caused shifts in the traits of the plant species, specifically in plant height and leaf thickness. These shifts were consistent with character displacement and niche differentiation (Fig. 1a). The researchers also observed ecosystem-level consequences of these rapid evolutionary changes: the mixed cultures of plants from the diverse

communities were more productive in terms of biomass than were mixed cultures from monocultures. These results exemplify the emerging field of eco-evolutionary dynamics, which emphasizes that not only does ecology drive evolution, but evolutionary change feeds back to affect ecological processes⁵.

In Zuppingger-Dingley and colleagues' study, laboratory propagation of the plants increased the chance that the differences between the high- and low-diversity selection groups were due to genetic divergence. However, it is possible that epigenetic factors — heritable changes that do not involve DNA-sequence changes — could have had a simultaneous role⁶. If so, this invokes a broader question⁷ concerning the influence of developmental plasticity in niche differentiation: might character displacement in a diverse community initially be driven by developmental responses to resources and competitors that are later genetically assimilated as speciation occurs? The present study suggests that this challenging question could be addressed in real time with an experimental, field-based approach.

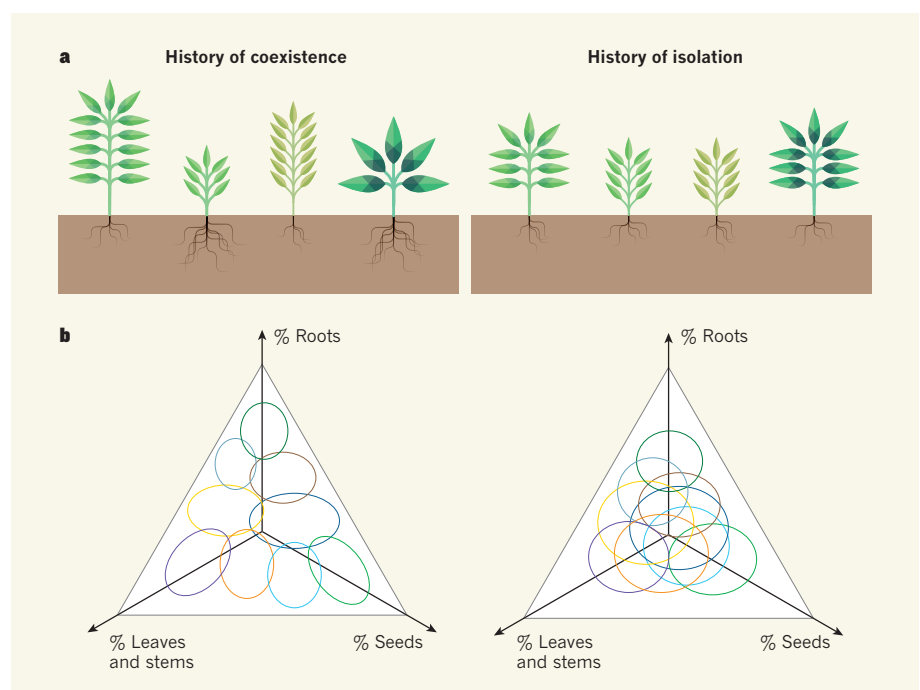


Figure 1 | Evolutionary niche shifts. **a**, Zuppingger-Dingley *et al.*¹ find that, when plant species are grown in a common environment, those that have a history of selection in diverse communities develop greater differences in traits (such as height and leaf thickness) than species that have a history of isolation. **b**, This idea feeds into our understanding of how evolutionary history influences the ecological interactions of species that compete for growth factors such as soil nutrients, light and space. All species face trade-offs. For instance, biomass that is allocated to obtaining soil nutrients (roots) cannot be used to obtain light (leaves and stems) or to disperse to open sites (seeds). Graphically depicted, the resulting 'trade-off surface' (triangles) represents all possible ways in which plant species (ellipses) can allocate their biomass. A history of selection in diverse communities results in greater interspecific differences (less overlap of ellipses) and more specialization (smaller ellipses) than a history of isolation.

Because natural communities are diverse, selective forces that emerge from interactions between many species may be unexpectedly influential factors that shape species traits. How might we conceptualize this possibility? Stable coexistence requires both character displacement and evolutionarily unavoidable trade-offs between species^{8,9}. Such interspecific trade-offs occur only if allocation of biomass to traits that increase performance in one type of environment decreases performance in other environments. For example, plants that have greater root mass perform better in infertile soils, but those that have more leaf and stem mass — and thus are taller and capture more light — dominate fertile soils. Such trade-off ‘surfaces’ could explain how the

ecological interactions that allow multi-species coexistence also influence the rate and pattern of species formation^{8,9} (Fig. 1b).

Although the disciplines of ecosystem ecology and evolution have developed their own perspectives, if each incorporated elements of the other, both disciplines would be strengthened. It is time for a reunification of all of the branches of natural history in a renewed search for unified explanations of the patterns seen in the natural world. ■

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1. Zuppinge-Dingley, D. *et al.* *Nature* <http://dx.doi.org/10.1038/nature13869> (2014).
2. Lehman, C. L. & Tilman, D. *Am. Nat.* **156**, 534–552 (2000).
3. Rainey, P. B. & Travisano, M. *Nature* **394**, 69–72 (1998).
4. Grant, P. R. & Grant, B. R. *Science* **313**, 224–226 (2006).
5. Fussmann, G. F., Loreau, M. & Abrams, P. A. *Funct. Ecol.* **21**, 465–477 (2007).
6. Verhoeven, K. J. F., Jansen, J. J., van Dijk, P. J. & Biere, A. *New Phytol.* **185**, 1108–1118 (2010).
7. Pfennig, D. W. *et al.* *Trends Ecol. Evol.* **25**, 459–467 (2010).
8. Tilman, D. *Proc. Natl Acad. Sci. USA* **101**, 10854–10861 (2004).
9. Tilman, D. *Am. Nat.* **178**, 355–371 (2011).