The importance of biodiverse plant communities for healthy soils

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With the recent focus on climate change at COP-26, the spotlight has, understandably, temporarily moved off the myriad other environmental challenges humanity faces—many of them interlinked. Among these are the ongoing loss of biological diversity and threats to soil fertility. In PNAS, Furey and Tilman (1) present results from a long-term field experiment that demonstrates the importance of plant diversity for healthy soils.

Although the issue dates back to Darwin (2), ecologists only really started to intensively study the importance of biodiversity for ecosystem functioning in the early 1990s—an idea that was initially controversial and heavily debated until a series of review and consensus pieces started to provide some clarity and agreement (3–8). One of the key approaches employed was the use of biodiversity experiments: interventions that directly manipulate numbers and types of species while monitoring the response of ecosystem functioning—changes in the stocks and flows of energy and matter. These biogeochemical processes—like primary productivity—underpin human societies by providing a multitude of ecosystem services (or "nature's contributions to people"), such as the provision of food, materials, and clean water; the sequestration of atmospheric carbon; and the generation of healthy soils. Furey and Tilman (1) present results from the longest-running biodiversity experiment (it will soon celebrate its 30th anniversary in 2024) that show how ecologically diverse mixtures of plant species can generate soils that are richer in essential plant nutrients and more productive in plant biomass and that store more carbon.

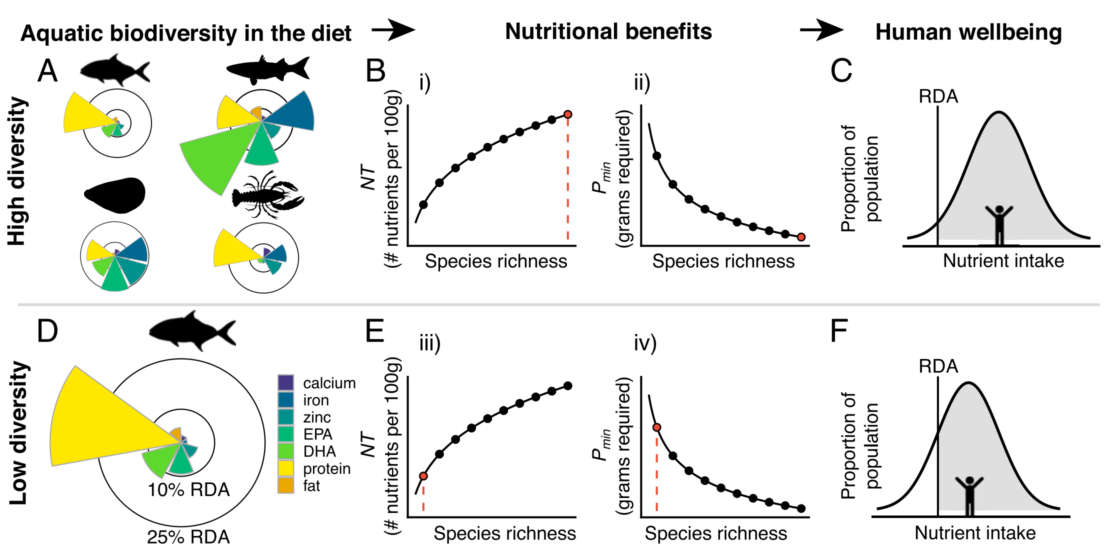

Fig. 1. Complementary nutrient profiles of diverse marine animal communities, with the healthier diets that they provide (19), have similarities with the complementary nutrient profiles of diverse plant communities found by Furey and Tilman (1) that generate healthier soils. Because multinutrient profiles are positively related to the richness of marine species, increases in aquatic biodiversity increase human well-being through nutritional benefits (*A–C* vs. *D–F*), including the number of recommended daily allowance (RDA) nutrient targets (NTs; 10 and 25% thresholds of RDA guidelines) met and smaller seafood requirements (*B, i* and *E, iii* vs. *B, ii* and *E, iv*). DHA, docosahexaenoic acid; EPA, eicosapentaenoic acid. Reproduced from ref. 19.

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To manipulate plant diversity at their study system in the prairies of the Cedar Creek Ecosystem Science Reserve in Minnesota, the preexisting seed bank had to be removed so that designed mixtures of plants could be sown that experimentally varied numbers and types of species. While it has its drawbacks, the removal of the topsoil brought the opportunity to monitor the development of the soils under the different diversity plant communities. Twenty-three years after inception, the more diverse plant communities had generated soils that were richer in several soil nutrients, including nitrogen, potassium, calcium, and magnesium (phosphorous, which was at consistently high levels in these ex-agricultural former prairie soils, was an exception). The soils under the more diverse plant communities also stored more carbon and generated conditions normally considered indicators of a healthy soil (from a human perspective): a higher cation exchange capacity and less acidic pH.

Although soil development is a complex process that is not fully understood, the controlled nature of the designed experiment that manipulated plant diversity while holding other conditions constant makes it possible to start to understand the processes that led to the generation of healthier soils. The higher levels of these elements in the soils under the more diverse plant communities were associated with increased amounts of the same nutrients in the plant biomass, both above- and belowground. The inference is that more diverse plant communities are better at capturing essential plant nutrients from the soil, leading to greater biomass production and larger pools of these nutrients that are then released back to the soil in the longer term as plants senesce and die, increasing soil fertility. By wiping the slate clean and then manipulating plant diversity, the experiment appears to reveal a virtuous circle where over nearly a quarter of a century, higher plant diversity led to better nutrient uptake and retention, more productive plant communities, and more fertile soils. In general, levels of all nutrients increased over time from 1994 to 2017 but only modestly in single-species monocultures and progressively more as numbers of plant species in the experimental plots increased. Potassium provides an interesting exception where levels in monocultures in 2017 were lower than at the start of the experiment, suggesting that single-species plots can sometimes lose soil resources over time. These results, which complement earlier findings from the same project (9), also emphasize the importance of long-term experiments when studying ecological processes that takes years to fully develop.

Plant biomass is mainly carbon (and water), and carbon alone is not enough to produce fertile, healthy soils, which depend on multiple plant nutrients and favorable soil conditions. A second design feature of the Cedar Creek biodiversity experiment makes it possible to go further in understanding how diverse plant communities are able to outperform depauperate versions in terms of their nutrient profiles. As well as manipulating numbers of plant species (from monocultures up to mixtures combining 16 species), the plant communities vary in their composition in terms of three commonly used plant functional groups that separate grasses, nitrogen-fixing legumes, and other herbaceous species (or forbs). It is ecological differences among species that seem to enable diverse mixtures to do better overall, with those from different groups specializing in uptake of different nutrients and in emphasizing biomass production either above- or belowground. Diverse communities with species from all three functional groups were able to accumulate higher levels of nitrogen, potassium, calcium, and magnesium in soil and vegetation than any single group could achieve on its own.

These functional group results beg the question of how much biodiversity we need to generate fertile soils. Are mixtures of two or three species sufficient? Are the other species functionally redundant? This is a hard question to definitively answer without comparing all possible mixtures of species in a well-replicated experiment—something that is logistically not feasible. However, the linear relationships of productivity and soil responses with plant diversity suggest this may not be the case. It is also hard to be sure about when a species is fully redundant—species that may appear unimportant at one point in time may play a role in the stability of ecosystem functioning in the long term (10). Earlier studies considering multiple ecosystem functions (including some soil nutrients and conditions) have found that the more ecosystem responses that are considered, the more species are found to play a supporting role (11), something that is also true as studies consider greater spatial and temporal scales where different species seem to play functionally important roles at different times and places (12). The work of Furey and Tilman (1) suggests the same may be true when examining multiple soil processes—but how many of the prairie species are needed for a healthy soil remains an open question (to which I return below).

Although the paper of Furey and Tilman demonstrates the limitations of monocultures, it also raises the question of how many species are functionally important. Would mixtures containing just one species of grass, legume, and forb be enough as far as healthy soils are concerned?

Another unknown is the role played by biodiversity within the soil microbial community. The Cedar Creek biodiversity experiment manipulates the diversity of plants, but a similar approach has previously shown important effects of the diversity of mycorrhizal fungi. Back in 1998, a collaborative team of researchers performed the same type of biodiversity experiment in a similar North American old-field ecosystem (13). The crucial difference was that instead of varying the numbers of plant species, they manipulated the number of species of native arbuscular mycorrhizal fungi. Increasing the number of mycorrhizal species led to increases in plant diversity, above- and belowground biomass production, and soil phosphorous levels. Taken together, these results from biodiversity experiments that manipulate different groups of organisms suggest potential feedbacks in which the diversity of one group can support the diversity of another with beneficial effects for the ecosystem, including its soils. How to best tease these complex interrelationships apart will provide a rich seed bed for new ideas for future research, not just in grassland but also, in less well-studied ecosystems from forests (6, 14–16) and hopefully, to coral reefs and beyond.

Other past research suggests that what goes for plants may sometimes go for animals too. In pasture grassland ecosystems in Japan and Mongolia, chemical analysis of aboveground plant biomass suggests that more diverse plant communities provide a better balance of minerals for domesticated grazers (17, 18). More recently, Bernhardt and O'Connor (19) assembled a large database on nutrient (and harmful contaminant) concentrations for several hundred species of fish and other aquatic animals. Their real-world results resonate with those from the Cedar Creek biodiversity experiment. They find that because different species have different nutrient profiles (for iron, zinc, calcium, and fatty acids), diverse aquatic animal communities support diverse seafood diets that should be better for human health and well-being (Fig. 1).

The results from Cedar Creek suggest that diversification may provide a potential nature-based solution to several environmental challenges. The work raises the possibility that increasing the number and range of species used for grassland management and restoration may not only increase levels of biodiversity but also, improve soil health and the multiple benefits it can bring. Diversification could be applied in several settings from grazing pastures to cover crops and crop rotations to intercropping and sustainable feedstocks for biofuels to the restoration of prairies and other grasslands (20).

After a slow start, research on the relationship between biodiversity and ecosystem functioning is now well developed, with more than a quarter of a century of intensive modern work. The question remains as timely and pressing as ever given the ongoing loss of biological diversity. A constant during this period—presumably due to the initial controversy—has been the need for biodiversity to justify itself by demonstrating significantly better functioning than monocultures. Although the paper of Furey and Tilman (1) demonstrates the limitations of monocultures, it also raises the question of how many species are functionally important. Would mixtures containing just one species of grass, legume, and forb be enough as far as healthy soils are concerned? However, times are changing, and diversification is increasingly being seen as a benefit in its own right alongside its other potential advantages, including impacts on ecosystem functioning. This raises the question of how we strike the balance between diversity and function. Is diversification desirable in its own right even if it does not bring clear functional gains? In some cases, would we even be willing to bare some reduction in functioning in order to increase levels of diversity? How many species we need in our ecosystems for their functional and nonfunctional roles and how to best strike the balance remain as live an issue as ever.

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