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Ecology

Herbivores drive scarcity of nitrogen-fixing plants

Joy B. Winbourne & Lindsay A. McCulloch

In mature tropical forests, trees that can capture nitrogen experience high levels of herbivory. This could explain the low abundance of such trees, and demonstrates that herbivores can limit nitrogen availability on land. **See p.483**

Terrestrial ecosystems have a key role in helping to slow the pace of climate change, absorbing roughly one-third of the carbon dioxide emissions produced by human activities since the start of the Industrial Revolution[1]. However, the extent of this uptake of carbon on land is limited by the availability of nitrogen[2] — a phenomenon that has puzzled scientists for decades[3]. On page 483, Barker *et al.*[4] present data to address a long-standing hypothesis[3] that herbivory explains nitrogen limitation.

Several plant species in the legume family, including peas, have evolved partnerships with bacteria that can capture (also termed fix) nitrogen from the atmosphere and convert it into molecules that are the building blocks for amino acids and DNA. Trees that host these symbiotic bacteria (called nitrogen-fixing trees, or nitrogen fixers) have a competitive advantage when nitrogen is in limited supply[5]. Yet, despite this advantage, nitrogen fixers comprise only 5–15% of the trees in mature tropical forests[6]. Solving this paradox will improve our understanding of nutrient cycling in forest ecosystems and will also advance our ability to correctly predict the extent of terrestrial carbon capture[7].

Previous studies examining the puzzle of nitrogen limitation on land have pointed to constraints on the availability of light and nutrients as influencing legume growth and nitrogen-fixing activity. Nitrogen-fixing trees are more competitive than are trees that don't fix nitrogen during periods in which light availability and demand for nutrients are high[8–10], such as the early stages of forest development, or when a large tree falls and creates a gap in the canopy that can be filled. However, in mature tropical forests, these explanations seem insufficient to explain the low abundance of nitrogen-fixing trees. Theory[11] and some experimental studies[12] show that tropical legumes can turn off nitrogen fixation in some conditions, making nitrogen-fixing trees equally competitive with non-fixers[11]. However, if herbivory (Fig. 1) is greater among nitrogen fixers than among non-fixers, this could result in a cost that is sufficient to restrict the growth, survival and abundance of nitrogen-fixing plants in tropical forests.

Barker and colleagues tested whether nitrogen-fixing trees experience higher levels of herbivory than do non-fixers, and modelled the carbon cost of this herbivory. In a field study, the authors examined diverse tree species (23 species capable of fixing nitrogen and 20 non-fixers) growing as understorey seedlings in mature tropical forests in Barro Colorado Island, Panama. Barker *et al.* report that nitrogen fixers are targeted 21% more often by herbivores than are non-fixers, which results in a carbon cost for nitrogen fixers that is nearly twice as high as that for non-fixers. In modelling the carbon cost, the authors considered the loss of carbon in leaf tissue that must be replaced and the opportunity cost that results from that lost leaf material no longer making carbon-rich sugars by photosynthesis. Barker *et al.* suggest that the substantial carbon cost explains why nitrogen-fixing trees are not as abundant as might be expected in mature tropical forests.

Surprisingly, nitrogen fixers' high herbivory rates could not be accounted for by a range of leaf physical and chemical characteristics that the authors examined. At first, this seems counter-intuitive. Several studies, including this one, show that nitrogen fixers have higher concentrations of nitrogen in their tissues than do non-nitrogen-fixing plants, even when

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Figure 1 | Herbivory of leaves on trees in Barro Colorado Island, Panama.

From the archive

Efforts to understand human memory, and ants manage to cultivate fungi as a food source.

50 years ago

Organization of Memory. Edited by E. Tulving and W. Donaldson — It is ... the organization of our knowledge that makes possible the use of that knowledge in mental processes and behaviour. The fact that information is stored is clearly a prerequisite, but if memory were simply retention, and knowledge were simply stored like so much furniture in a warehouse, it would be useless. Evidently information is organized to reflect its semantic significance, and it is this that makes such human activities as thought and language possible. This book is fascinating because much of the material in it is related to this issue which might be thought of as one of the most important in psychology at present ... Because ... some aspects of memory ... are measurable, many experimental psychologists have chosen to start with these. Thus success in recalling lists of words can give clues as to how the remembered material is organized ... One might indeed wonder why, if memory is so important for human intelligence, human performance on memory tasks is so feeble.

From *Nature* 15 December 1972

100 years ago

It is scarcely possible to grasp the true ecological significance ... of the extreme cases of apparent or true symbiosis, between certain ants and ... plants. In a recent ... publication ... J. Bequaert has brought together the varied and disconnected links of existing knowledge ... In Europe a great many grasses ... rely almost exclusively ... on certain species of ants for the successful dissemination of their seed. The cultivation of fungi by ants is one of the curiosities of biology ... [W]hen the female of *Atta sexdens* starts a new colony, she carries ... a pellet containing fungal hyphae, with which to start fungus cultivation. She manures the mycelium until it attains a sufficiently luxurious growth to feed to the larvae.

From *Nature* 16 December 1922

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they are not actively engaging in nitrogen fixation[13] — a scenario that was probably the case for the understorey seedlings examined Barker and colleagues. It would be expected that herbivores might choose nitrogen fixers for the tasty nitrogen-rich leaves, and that this characteristic would correlate positively with herbivory. However, plants can also invest their nitrogen in processes that generate chemical defences, which could deter herbivores[14]; this might suggest a negative correlation between herbivory and such chemical defences.

The fact that the study identified no relationship between herbivory and plant characteristics that are thought to influence herbivory dynamics is compelling. The authors suggest that this points to co-evolutionary relationships between legumes and herbivores. Such relationships could emerge from reciprocal interactions as herbivores focused on legumes for nitrogen-rich leaves, and legumes responded with alternative species-specific chemical and physical plant defences. Over time, herbivores might evolve to favour nitrogen fixers on the basis of species-specific traits that now seem to be independent of the original connection to plant nutritional status. This hypothesis should be assessed with regard to the potential co-evolution between legumes and herbivores, and studies performed to ascertain how this evolutionary relationship affects the nitrogen and carbon cycles of tropical forests.

> **“The substantial carbon cost explains why nitrogen-fixing trees are not as abundant as might be expected.”**

Barker and colleagues’ results constitute a notable shift from current proposed explanations for the nitrogen paradox, and highlight several areas for further inquiry. The study examined an impressive number of neotropical legume species — nearly all of the species of legume that are found at this site in Panama. However, this represents just a small fraction of the diversity of legume species found throughout the tropics[15]. It will be interesting to consider how herbivory pressure on nitrogen fixers differs among tropical forests around the globe (including ‘wet’ compared with ‘dry’ tropical forests), between different communities of legumes and herbivore species, and across different stages of a plant’s life.

The seedling stage examined in this study is a key time for determining which individuals become established, remain in the forest community and grow into mature forest canopy trees. In closed-canopy, mature tropical forests, canopy gaps that increase the light that reaches the forest floor are especially crucial for the development of seedlings that will ultimately become canopy trees. Nitrogen-fixing trees in these forest gaps have high rates of nitrogen fixation[10]. How do herbivore pressures differ between seedlings found in the shade of canopy trees and those found in gaps in the forest canopy that have high light availability? Does herbivory vary between trees in these forest gaps that differ in their rates of nitrogen fixation?

At what point in the life of a tree does herbivory create a carbon cost sufficient for the tree to turn off nitrogen fixation, and how does this biological pressure interact with known physical controls on nitrogen fixation? Future studies that link differences in herbivory pressure with direct measurements of nitrogen fixation and the plant’s corresponding carbon-allocation strategies will help to elucidate the influence of herbivory on tropical nutrient cycles.

Barker and colleagues’ study is one of the first to assess whether herbivory pressure is greater for tropical nitrogen-fixing trees than for non-fixers, and to suggest a mechanism that could explain the low abundance of legumes in neotropical wet forests. As Earth-system models begin to represent nitrogen fixation with the same level of detail as photosynthesis[7], consideration of biological constraints such as herbivory is needed, along with insight into known physical controls. Such information will be required to advance our understanding of how these tropical-forest systems will respond to climate change[7].

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