

Does phosphorus limitation promote species-rich plant communities?

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Abstract It is known that the number of limiting nutrients may affect the species richness of plant communities, but it is unclear whether the type of nutrient limitation is also important. I place the results from a study in Patagonia (elsewhere in this issue) in the context of the number and types of nutrients that are limiting. I present four mechanisms through which N or P limitation may potentially influence species richness. These mechanisms are related to: (i) the number of forms in which P or N are present in soil and the plant traits needed to acquire them, (ii) the mechanisms and traits that control species competition and coexistence under N or P limitation, (iii) the regional species pools of plants capable of growing under N- and P-limited conditions, and (iv) the interaction between the type of nutrient limitation and community productivity. It appears likely that P limitation can favour a higher species richness than N limitation, in at least in a variety of low productive plant communities, but evidence to support this conclusion is so far lacking. The four mechanisms proposed here offer a framework for exploring whether the type of nutrient limitation per se, or an interaction with productivity, is a potential driver for variation in species diversity.

Keywords N:P stoichiometry · Nutrient limitation · Diversity-productivity · Species competition · Species pool · Biodiversity · N:P ratio · Nitrogen · Phosphorus · Resource balance hypothesis · Growth rate hypothesis

Species richness of plant communities under N or P limitation

The species composition of plant communities when nitrogen (N) is the limiting nutrient is very different from that when phosphorus (P) is the limiting nutrient, even when the total productivity of the vegetation is identical. These different species compositions became very obvious in long-term fertilization experiments such as Park Grass (Tilman 1982), Rengen (Chytrý et al. 2009), or Černikovice (Honsova et al. 2007), where different grass species were found to dominate under N and P limitation, and legumes were more abundant under N limitation. From a biodiversity point of view, it is an interesting question whether the type of limitation also influences how many species may coexist and, if so, through what mechanisms? In fertilization experiments, both the addition of N and P can reduce species richness (Gough et al. 2000), but this is predominantly due to negative effects of higher biomass and more intense competition for light (Aerts et al. 2003; Beltman et al. 2007; Goldberg and Miller 1990). To evaluate whether the type of nutrient limitation influences species richness of plant communities, species richness in the field has been correlated

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with some measure of the relative availabilities of N and P. One of the measures commonly used in these studies has been the ratio of N:P in the aboveground vegetation. When experimentally calibrated for the type of vegetation, this ratio can be used as an estimator of the type of nutrient limitation (Güsewell 2004; Koerselman and Meuleman 1996; Olde Venterink et al. 2003; Cech et al. 2008).

In this issue of *Plant and Soil*, Blanck et al. (2011) show that total plant species richness in matorral shrub-lands in Patagonia, Argentina, decreases with increasing P availability, as indicated not only by concentrations of P in the soil but also by N:P ratios and P concentrations in the leaves of the common shrub *Berberis buxifolia*. These correlations with species richness are consistent with data from other studies. Thus, negative relationships with soil P have been reported from ecosystems in Australia (Lambers et al. 2010), Costa Rica (Huston 1980), Brazilian Cerrado (L. Lannes, unpublished data), and European grasslands (Janssens et al. 1998; Olde Venterink et al. 2001b), while positive correlations have been found with N:P in the vegetation for the Brazilian Cerrado (L. Lannes, unpublished data). However, other studies—mainly in grassland and wetland vegetation in Europe and North America—have shown a unimodal relationships, with species richness peaking at intermediate N:P ratios, and negative relationships have also been reported (Güsewell et al. 2005; Roem and Berendse 2000; Wassen et al. 2005). A meta-analysis would be very useful to evaluate whether differences in the ranges in N:P ratio and/or species richness of the different studies match each other (see below), or whether there is a general difference in species richness-N:P ratio patterns between old weathered soils and younger soils (Hopper 2009).

The unimodal relationship between species diversity and N:P ratios reported in some studies is consistent with the resource balance hypothesis, which predicts that species diversity will be highest at intermediate N:P ratios (Braakhekke and Hooftman 1999; Daufresne and Hedin 2005; Cardinale et al. 2009). The rationale for this hypothesis is that if community biomass production is limited by several resources, growth of individual species may be limited by different resources, and the species will therefore not exclude each other (Tilman 1982). This mechanism is likely to be more relevant for aquatic

ecosystems, where nutrients are well mixed, than for plants growing in soil, where nutrients are distributed heterogeneously (Huston and DeAngelis 1994); however, there is some evidence that it does apply also in terrestrial ecosystems (Harpole and Tilman 2007; Roem et al. 2002). In their study, Blanck et al. (2011) found that the N:P ratio in leaves of the shrub *Berberis buxifolia* ranged between 4–25 on molar base which corresponds to c. 2–12 on mass base. Despite this wide range in N:P ratios, they conclude that all their plots were probably N-limited. Although one should be careful to translate N:P ratios of a single species to that of the entire vegetation (Güsewell and Koerselman 2002), these low N:P ratios suggest to me that the pattern of increasing species richness with increasing N:P ratios, in fact, reflects a gradient from severe N-limitation towards N-P co-limitation (Güsewell 2004; Koerselman and Meuleman 1996; Olde Venterink et al. 2003; Cech et al. 2008), and hence would be consistent with the resource-balance hypothesis. However, the observed difference in species richness (c. 7 species) appears rather high if it is due only to the transition from one limiting nutrient to two limiting nutrients (Harpole and Tilman 2007).

Species richness patterns in relation to the type of nutrient limitation can be studied at different spatial scales and in different types of landscapes. The papers cited above, including (Blanck et al. 2011), are examples of studies performed at a local or regional scale. Furthermore, the study site of Blanck et al. in Patagonia is an example of a relatively young, often disturbed, fertile landscape (YODFEL; Hopper 2009). On a global scale, however, the most species-rich biomes—classified as ‘biodiversity hotspots’ and typically with many endemic species—occur mainly in old, climatically buffered, infertile landscapes (OCBILs) such as south-western Australia (Fig. 1a), the Cape Province in South Africa, and parts of tropical South America (Fig. 1b) (Hopper 2009; Myers et al. 2000). Lambers et al. (2010; 2008) suggested that in these old landscapes the vegetation is more likely to be P-limited, which could partly explain their high species richness (see below). If so—and more fertilization experiments are still needed to demonstrate this—conservation managers should assess not only the threat to these communities posed by N enrichment, as done by Phoenix et al. (2006), but also that posed by P enrichment.

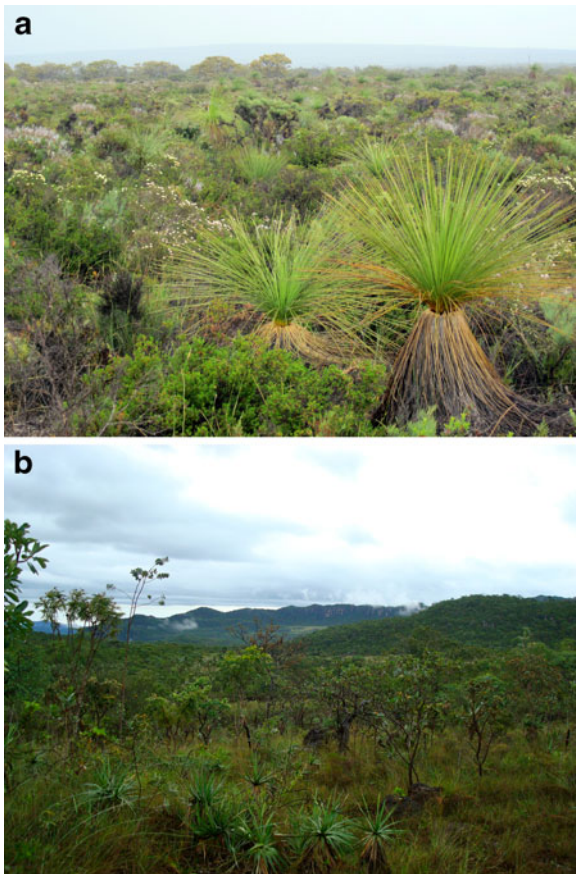


Fig. 1 Two examples of exceptionally species rich plant communities: **a** Kwongan vegetation in South West Australia (photograph Etienne Laliberté) and **b** Cerrado vegetation in Central Brazil (photograph Luciola Lannes). Both plant communities occur on old, climatically buffered, infertile landscapes under presumably P limited conditions

How to explain differences in species richness under N or P limitation?

Below, I describe four mechanisms by which the identity of the limiting nutrient(s) could affect species richness. These mechanisms are related to: (i) the number of forms in which P or N are present in soil and the number of plant traits to acquire them, (ii) the mechanisms and traits that control species competition and coexistence under N or P limitation, (iii) the sizes of regional species pools for N- or P-limited conditions, and (iv) the interaction between the type of nutrient limitation and community productivity. One or more of these might potentially explain why in particular P-limited conditions enable more species to co-exist than N-limited conditions, or vice versa. I

present these mechanisms to stimulate research to gain evidence for one or more of these mechanisms to support a higher species richness under either P or N limitation, and under which environmental conditions this may occur. These mechanisms are related to each other, either directly or through evolution, as illustrated in Fig. 2. Evolutionary relationships occur when related species possess plant traits enabling them to utilise particular forms of N and P, and may lead to regional pools of species with adaptations to N or P limitation.

- (i) *Numbers of forms of N and P in the soil and variation in plant traits to acquire them.* McKane et al. (2002) showed that different plant species in the arctic Tundra use different forms of N, and that the most abundant species also use the most abundant N forms. Such niche differentiation of species with respect to N forms was also demonstrated for some grasslands (Kahmen et al. 2006; Weigelt et al. 2005). Likewise, Turner (2008) hypothesized that different forms of P in soil also facilitate niche differentiation and coexistence of different species. It is only a small step further to suggest that the nutrient that has the highest variety of forms also facilitates the highest number of coexisting species. Both N and P can occur in a variety of inorganic and organic forms in soil. At any particular site, the number of forms is likely to depend upon rock type, history, and environmental conditions. I expect that in many environments the number of P forms will exceed the number of N forms, because of the large potential variety of chemical P complexes with, e.g., Ca, Mg, Fe, and Al compounds, as well as organic compounds as P-monoesters, P-diesteres, phosphonates, and polyphosphates (cf. Turner 2008). However, this assumption remains to be rigorously tested.

Exploiting the different forms of N and P in the soil requires different plant traits, including root morphological traits and physiological traits such as exudation of various organic acids and enzymes (see review of Richardson et al. (2009)). Lambers et al. (2008) showed that plant traits and strategies to acquire N and P change with soil age, with fast-growing nonmycorrhizal plants and plants with arbuscular mycorrhizal associations at the youngest soils to plants with

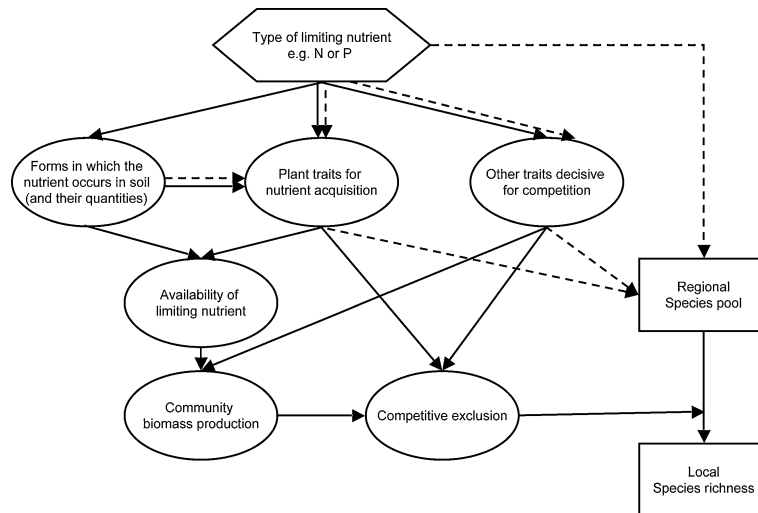


Fig. 2 Conceptual representation of how the type of limiting nutrient (e.g. N or P) can influence species richness on a regional scale (species pools) and local species richness. Dashed lines indicate evolutionary influences and solid lines direct influences in e.g. a local plant community; see text for

explanation. The basic concept how environmental conditions (such as the type of nutrient limitation) influence local species richness through their effect on the species pool and through community biomass production follows Gough et al. (1994)

cluster roots on the oldest soils. Just as for the number of forms in which N or P occurs in soil, it is unlikely that the numbers of traits to acquire N or P are identical. Instead, more traits and strategies have probably evolved for the nutrient that occurs in the largest variety of forms, especially if most forms are not readily available to most plants (cf. Turner 2008). From this, I would predict a greater diversity of uptake mechanisms for P than for N, though this assumption requires to be confirmed with data.

- (ii) *Traits influencing competition and coexistence.* An important process in plant competition is resource pre-emption. In the case of competition for nutrients, the superior competitor will acquire a resource from the rhizosphere more rapidly than its competing neighbours, and the total root length of the competing plants is the decisive trait to enable this (Craine et al. 2005). Indeed, Olde Venterink and Güsewell (2010) recently demonstrated that this pre-emption competition mechanism was supported for two competing grass species under N limitation, but not under P limitation. Under P-limitation, traits other than root length, such as root phosphatase activity and root mortality appeared to be more important for the outcome of competition for these two

grasses. These results fit well with other studies indicating that N limitation favours plants with a high biomass investment in roots and root length, and a high photosynthetic activity, growth rate and nitrogen productivity, in contrast, to P limitation where investments in P acquisition and storage, a long leaf life span, defences against herbivores, reduction of nutrient losses, and high nutrient-resorption efficiency are more decisive (Güsewell 2005a, b; Güsewell et al. 2003; Harrington et al. 2001; Lambers et al. 2010; Lambers et al. 2008; Treseder and Vitousek 2001). These different sets of traits favoured under N or P limitation could imply that belowground competition for nutrient acquisition may be less important under P limitation than under N limitation. The variety of mechanisms to avoid P losses or otherwise enhance P-use-efficiency may potentially act as fitness equalizing processes that might enhance the number of species that can potentially co-exist. Further research is needed to improve our understanding of the importance of plant traits for species competition under P and N limitation, and how these influence species richness.

- (iii) *Species-pool effects.* The size of the regional species pool is a measure for comparing species richness among regions at a global scale, and

also an important control upon species richness at a local scale (Pärtel et al. 1996; Huston 1999). The size of the species pool is thought to be affected by the historical opportunities for speciation, with higher species numbers under conditions that were formerly widespread (Zobel 1992). If N limitation was common in the relatively young, often disturbed, fertile landscapes (YODFELs) that are widespread in, but not restricted to, the Northern hemisphere, we would expect this to be reflected in a large pool of species adapted to these conditions. In contrast, if P limitation is associated with old, climatically buffered, infertile landscapes (OCBILs) (Hopper 2009; Lambers et al. 2008; Reich and Oleksyn 2004; Vitousek and Howarth 1991), we would expect the largest regional species pool under P limitation in the OCBILs. Güsewell et al. (2005) found that the regional species pool of European wetlands—i.e., an

example of YODFELs—was indeed higher under N limitation than under P limitation. Such species pool effects could potentially explain the decreasing or unimodal relationships between local species richness and vegetation N:P ratio in YODFELs, and increasing relationships in OCBILs (see above). The results from the Patagonian site (a YODFEL) of Blanck et al. (2011) would fit as part of the upward slope of a unimodal pattern between richness and N:P ratio, which corresponds with the very low range of N:P ratios they observed (2–12 on mass base).

(iv) *Interactions with vegetation productivity.* Productivity is an important controlling factor for species richness, and the type of nutrient limitation and the N:P ratio in the vegetation correlate with the biomass production of the vegetation (see Fig. 3). According to the concept presented in Fig. 3c, diversity-productivity curves might differ under N

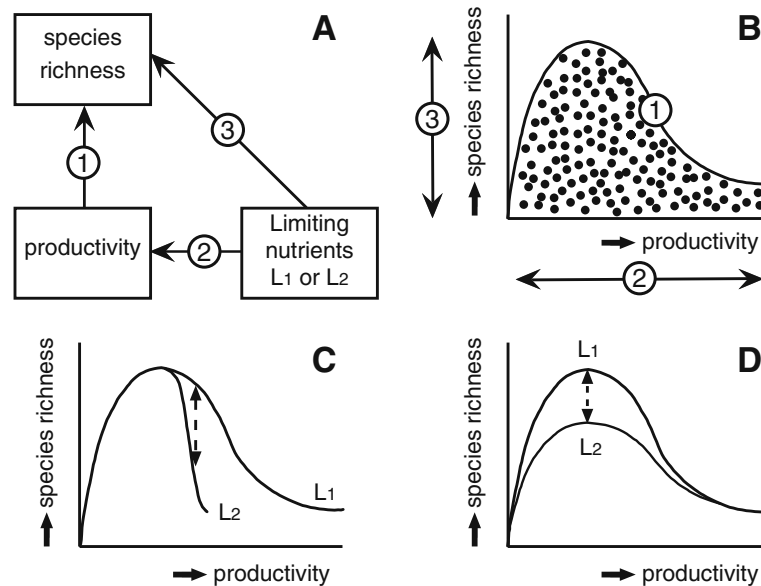


Fig. 3 Conceptual representation of how species richness-productivity patterns can be differentiated for plant communities that are growth limited by different nutrients (L1, L2). Panel B shows the hump shaped relationship observed in comprehensive field studies in wetlands in Canada, Europe and Siberia, which indicated that the line should be considered as the envelope enfolding a cloud of points (Grace 1999; Moore and Keddy 1989; Olde Venterink et al. 2003; Vasander 1982; Wassen et al. 2005; Wheeler and Shaw 1991). Hence maximum richness, and maximum variation in richness, are found at intermediate productivity. Panel C shows a possible differentiation because of variation in productivity levels ranges between

communities growth-limited by different nutrients, supported with data (Olde Venterink et al. 2003; Wassen et al. 2005) (see text). Panel D shows a possible differentiation because of variation in maximum species richness ranges, as a consequence of variation in regional species pool sizes under growth limitation by different nutrients (following Huston (1999)). 1=relationship between productivity and species richness, 2=effect of the kind of nutrient limitation on productivity, 3=effect of kind of nutrient limitation on species richness. The dashed arrows indicate possible effects of a shift from one limiting nutrient to another (Figure adjusted from Olde Venterink (2000))

and P limitation because of differences in productivity (i.e. variation on the x-axis). This postulate is supported by data from wetlands in Europe and Siberia, where maximum aboveground biomass (c. 1000 g m²) under P limitation (vegetation N:P ratio >16) was much lower than maximum aboveground biomass (c. 2800 g m²) under N limitation (vegetation N:P ratio <13.5) (Wassen et al. 2005). Although there is a pattern of decreasing N:P ratio with increasing productivity (Güsewell 2004, Wassen et al. 2005), which is consistent with the growth rate hypothesis (Elser et al. 2003), calibrations with fertilization experiments show that the N:P ratio can be used to predict the type of nutrient limitation up to an aboveground biomass of 1500 g m² (Olde Venterink et al. 2001a, b; 2003); hence a biomass clearly higher than the maximum biomass observed under P limitation by Wassen et al. (2005). Moreover, regression analysis using data for European and Siberian wetlands suggests that the diversity-productivity curve under P limitation is much narrower under P limitation than under N limitation (Wassen et al. 2005), just as hypothesized in Fig. 3c. This indicates (for these Eurasian wetlands, at least) that under intermediate to high productivity a higher species richness can be achieved under N limitation than under P-limitation (see dashed arrow in Fig. 3c). Further research is needed to investigate whether this pattern (Fig. 3c) also occurs in other areas and biomes, and about the mechanism(s) that might be responsible. The negative slope of Fig. 3b is usually explained through competitive exclusion for light (Grime 1979; Huston 1999; Hautier et al. 2009; but see also Dickson and Foster 2011). If this explanation is also valid for the two negative slopes in Fig. 3c - with the slope for P being much steeper than that for N (L2 vs. L1, respectively)—then we might conclude that species competition for light occurs across a narrower biomass range but is more intense under P than under N limitation. This hypothesis based upon Fig. 3c would be worth testing experimentally.

Furthermore, Huston (1999) predicted that the influence of regional species pool sizes on local species richness is related to productivity and disturbance; applying this idea to different growth limiting nutrients yields the patterns visualized in

Fig. 3d. Environmental factors as acidity, salinity of flooding can influence species richness—productivity patterns as illustrated in Fig. 3d (Grime 1979; Gough et al. 1994; Grace 1999), whether the type of nutrient limitation has a similar effect depends partly on whether regional species pool sizes differ between limiting nutrients (mechanism iii).

The patterns in Fig. 3c and d clearly illustrate that if a diversity-productivity pattern as illustrated in Fig. 3b hides different relationships for N or P limited conditions, a shift from one limiting nutrient to another can have severe effects on local species richness (Huston 1999; Olde Venterink et al. 2003).

Does P-limitation promote a higher species richness than N-limitation?

It is not unlikely that mechanisms i and ii might promote a higher species richness under P limitation than under N limitation, but the evidence for this still has to be provided (see above). However, interactions with productivity (mechanism iv), and evolutionary aspects (mechanism iii), suggest that if P limitation promotes a higher species richness it will be restricted to plant communities of low productivity, and more likely to occur in landscapes with ancient soils (OCBILs) than in those with young soils (YODFILs). Nevertheless, even in biomes where maximum species richness is the same under N or P limitation, endangered species may persist better under P-limited conditions, as was demonstrated for European meadows and fens (Olde Venterink et al. 2003; Wassen et al. 2005). This observation, as well as the supposed higher species richness under NP co-limitation than under conditions where just one nutrient is limiting (resource balance hypothesis; Braakhekke & Hooftman 1999; Harpole and Tilman 2007), provokes the question of whether it might be possible to promote species richness in N-limited sites by fertilizing them with N to produce conditions of P limitation or NP co-limitation (see Aerts et al. 2003; Güsewell et al. 2005). However, this idea is to be rejected; many studies show that species richness declines after N enrichment—whether from fertilizer or atmospheric deposition—and rare species tend to be replaced by common ones (Bai

et al. 2010; Bobbink et al. 2010; Clark et al. 2007; Stevens et al. 2010; Suding et al. 2005). By far the best way to conserve species in plant communities under P limitation is to prevent enrichment of both N and P. But this requires an understanding of the major biogeochemical processes affecting the availabilities and stoichiometry of these nutrients, and also of the influence of management (Cech et al. 2008; Olde Venterink et al. 2006; 2009). For instance, re-wetting of drained wetlands in order to reduce N mineralization rates and N availability may cause a strong P release and a strong negative effect on species diversity (Olde Venterink et al. 2002; Smolders et al. 2008; Van Dijk et al. 2007; Zak and Gelbrecht 2007).

Despite a long tradition of research on plant species richness in relation to nutrient availability and productivity, this commentary illustrates that much about these relationships is still unclear, particularly when comparing N-limited with P-limited conditions. The four mechanisms presented above, by which the identity of the limiting nutrient (N or P) can potentially affect species richness, are intended as challenges for future research. More information is required about the forms of N and P under different conditions, as well as about the plant traits and mechanisms needed to acquire these nutrients. We also need a better understanding of the mechanism of species competition under P limitation: which plant traits are decisive, and do these traits enable a greater species diversity than the set of decisive traits under N-limitation? Furthermore, hardly any data are available on regional species pool sizes of species adapted to N-limited or P limited condition in biomes with different geological and evolutionary histories. Finally, we need to understand better how the type of nutrient limitation might interact with species richness–productivity patterns, and the mechanisms behind these patterns. To start with, more studies like that of Blanck et al. (2011) are needed to provide the material for future meta-analyses.

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