Land-plant ecology on the basis of functional traits

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The tissue traits and architectures of plant species are important for land-plant ecology in two ways. First, they control ecosystem processes and define habitat and resources for other taxa; thus, they are a high priority for understanding the ecosystem at a site. Second, knowledge of trait costs and benefits offers the most promising path to understanding how vegetation properties change along physical geography gradients. There exists an informal shortlist of plant traits that are thought to be most informative. Here, we summarize recent research on correlations and tradeoffs surrounding some traits that are prospects for the shortlist. By extending the list and by developing better models for how traits influence species distributions and interactions, a strong foundation of basic ecology can be established, with many practical applications.

Schimper world and Hubbell world

Our world view follows Schimper [1]. In Schimper world, different plant species are more successful in different parts of the landscape, and this is because they have different quantitative traits, such as leaf nitrogen concentrations, rooting depths, wood densities, leaf sizes and potential canopy heights. Schimper world is set in real physical geography, along gradients of rainfall, temperature, and geomorphology.

Plant stems, canopy architecture, foliage and litter are so influential in terrestrial ecosystems that Schimper world should be important for any ecologist. For example, the partitioning of rainfall among interception loss, infiltration and runoff is strongly influenced by canopy and litter properties. Habitat for all resident species is created or modified by the physical traits of plants and their 3D layout (e.g. the wind speeds that move fungal spores; the leaf and twig sizes available for galls and leaf miners; the line of sight for an insectivorous bird; the daily range of temperatures for animals operating at the ground surface; and the depth and texture of litter for invertebrates). Albedo and turbulent gas exchanges with the atmosphere are influenced by the total leaf area, its texture and its vertical profile. Carbon assimilation, herbivory and cycles of mineral nutrients are products of leaf traits such as nutrient concentrations, photosynthetic capacities, chemical defences, engineering toughness and lifespans. These traits are important not only in live

leaves, but also through their influence on litter decomposition and nitrogen mineralization.

Thus, addressing the questions of how and why plant traits and architectures vary among species and sites is the most important single step towards understanding land-ecosystem properties in general. This might seem an obvious point, but Schimper world currently gets less attention than what could be called Hubbell world. Hubbell's 2001 book [2] was heralded by a special commentary in *Science* [3], has been debated and tested (e.g. [4,5]), and has had special-issue treatment in *Functional Ecology* [6]. The Hubbell question is about the rank-abundance curve that describes dominance, the species richness at a site of given size, and the species–area curve that describes how fast new species are encountered as the sample is extended spatially. In Hubbell world, species are said to be equivalent: they have equal per-individual chances of birth, death, dispersal and speciation. The physical landscape is unspecified and undifferentiated, with species equally competent throughout.

In Hubbell world, ecological-trait differences among species are deliberately removed from consideration. Although this is at one extreme of the spectrum of community theory (Box 1), much theory is directed towards species diversity rather than towards species physical traits, in spite of doubts over whether diversity outcomes are informative about the different ecological processes operating [7,8]. Also, few theory strands specify the location of the site in physical geography. Indeed, there would seem little value in specifying a physical environment without also specifying something about the ecological traits of the species; but a community theory that says nothing about patterns across real physical geography must surely be regarded as incomplete.

Schimper world and Hubbell world formulate different questions, rather than being alternative answers to the same question. Even if Hubbell world becomes generally accepted as the right model for species richness and abundances, it will still say nothing about plant species traits, physiologies and physiognomies at a site. We suggest that the Schimper questions are of the utmost importance for ecology, both theoretically and practically.

The Schimper questions are as yet unanswered, but two essential foundations for those answers are currently being established. The first is a strong cost–benefit understanding of key plant traits, so that one can understand how the competitiveness of different trait

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values shifts along physical geography gradients. The second foundation is data sets and models on a world scale. These put physiological studies from particular habitats, growth forms or clades into worldwide context. We comment on data sets and models, before turning to the state of knowledge about costs and benefits of some key traits.

Data sets and models

Data sets about species traits are approaching global coverage, following decades of effort from many contributors. Seed mass data now cover >12 000 species [9], wood anatomy >5000 species (http://insidewood.lib.ncsu.edu/) and leaf economic and stoichiometric data >2000 species [10–12]. The distributions of species are becoming better characterized as data sets of point locations rather than as presence or absence in grid squares (e.g. http://salvias.net/pages/, http://nvs.landcareresearch.co.nz/ and http://vegbank.org/vegbank/index.jsp). Global mapping of climate and soils (e.g. http://www.daac.ornl.gov/) is now at finer resolutions, although estimates at point locations remain less convincing for soils than for climate.

Global vegetation models exist that work from basic processes and that reproduce the main zonation of world vegetation (e.g. [13–15]). However, these models are not usually recognized as achievements of community ecology. They are fairly incomplete, as yet: they work in terms of plant functional types, such as 'broad-leaved evergreens' and 'C3 grasses and forbs'; information about quantitative traits is chopped into these rather broad categories rather than handled as continuous variables; only some of the important quantitative traits are modeled; and they identify dominant plant types but say little about the

spread of trait values within a vegetation type. Still, the models do provide a foundation for working from world databases for the physical environment, through cost–benefit models and onward to predictions for plant traits.

Ecologically significant plant traits and their variation across species

Because conceptual strategy dimensions such as competitiveness or shade tolerance are difficult to compare across habitats, recent plant strategy thinking (e.g. [16–22]) has often emphasized measurable traits. These trait dimensions provide the means to compare species worldwide. Nevertheless, individual traits should not be considered in isolation, because pairs of traits are often coordinated (Box 2). An important part of trait research addresses interrelations among different traits (e.g. [23]), quantifying the correlations and asking why some sets of traits are sufficiently closely coordinated to be thought of as forming a single dimension of strategy variation compounded from several traits.

Box 3. Trait variation among coexisting species is substantial

Although site-average leaf mass per area (LMA) shifts predictably along regional and global gradients of rainfall and temperature, these shifts are often smaller than the range of variation seen among coexisting species (Figure I). Seed mass ranges 10^5- or 10^6-fold across coexisting species [17]. Within-site variation accounts for large fractions of total worldwide variation for leaf lifespan (57%, variance components analysis), dark respiration (67%) and potential photosynthetic rate (48%) [10].

In other words, much of the trait variation between species is associated with different lifestyles within a common environment. Species traits are not unilaterally determined by the physical environment at a site, although it presumably filters out some trait values that are inviable there and frames the conditions for competition.
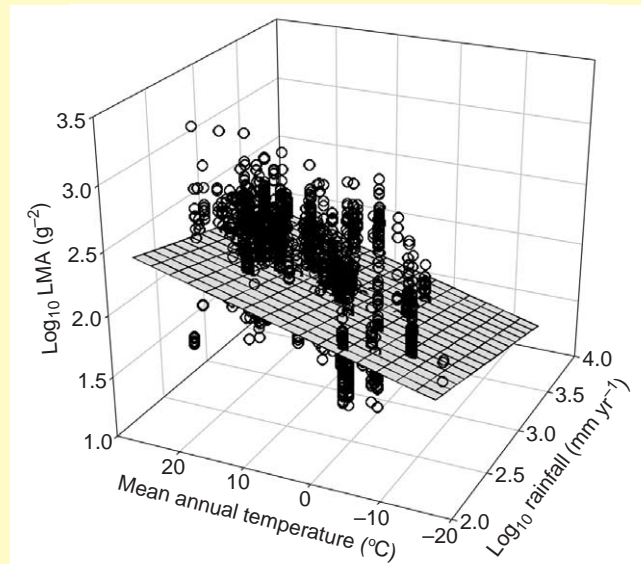

Figure I. Worldwide LMA in relation to mean annual temperature and mean annual rainfall. The tilted plane shows site-mean LMA responding to mean annual temperature and to rainfall. The vertical columns of dots show the spread of LMA values for individual species within each site. Reproduced with permission from [10].

For most traits, the spread of values observed across species within a site is wide (Box 3). This shows that a variety of ecological styles operate at any one site. The physical environment can be considered as filtering [24,25] the kinds of species that can succeed at a given site, or as setting the framework of total leaf cover and net primary production within which species interact, but not as exclusively determining the trait values that are present.

The research agenda for plant functional traits can be thought of as a developing short list of trait dimensions [17]. Ranking involves several criteria, including: practical measurability; application to ecosystem processes and to understanding species distributions; a firm understanding of the costs, benefits and physiology; and contributing information that is independent from other dimensions. Opinions vary, but three trait dimensions are now widely accepted as important ([26,27; reviewed in [17]):

- A 'leaf economic spectrum' [10,28] runs from species with cheaply constructed leaf area but

short-duration return on investment, to species with high leaf mass per area (LMA) and long leaf lifespan. Higher nitrogen and phosphorus concentrations and faster gas exchange rates are associated with the lower LMA end of the leaf economic spectrum. Herbs, grasses and deciduous trees tend towards the lower LMA end and evergreen shrubs and trees towards the higher LMA end, but there is wide overlap between growth forms.
- There is a spectrum where species with larger seeds have lower seed output per m^2 of canopy but better survival per week during early seedling life, under a variety of seedling hazards [17].
- There is a spectrum of canopy height at maturity, with taller final height trading off with rapid early height growth or with tolerance of low light [29,30]. It is an interesting and open question as to how this spectrum of potential height across species is related to allometric size scaling (Box 4).

Here, we review some further traits, chosen because rapid progress is being made, although much remains undetermined.

Xylem hydraulics, wood density and leaf size

Baas *et al.* [31] discussed xylem evolution within the framework of a 'tradeoff triangle'. Conductive efficiency

Box 4. Allometric size scaling in relation to ecological strategies of species

Can plant size usefully be thought of as one of the main dimensions of ecological strategy variation among species? Power laws that interrelate different size components of plants have a venerable history and, recently, there has been a fresh burst of activity (reviewed in [82,83]), where a theory about distributive networks in vasculature gives rise to characteristic scaling powers of 4/3 or 3/4. Scaling theory has been used in conjunction with general dimensional arguments [82,83], with metabolic arguments [84] and with observed data [82,83]. There is ongoing debate about scaling theory and its fit to data. Our aim here is not to join in that debate, but rather to assess the relationship between size scaling and other dimensions of ecological strategy variation among species.

Growth and metabolic rates for species have traditionally been expressed per unit of active tissue, for example net assimilation or photosynthetic rates per gram of leaf dry mass. In this formulation, it is implicit that as well as species-characterizing rates per unit leaf, one would also need a list of the amounts of leaf per species, to obtain rates per individual or per unit ground area.

Scaling theory similarly assumes that growth rates are per unit leaf mass. The difference is that scaling theory focuses on the size of individuals as a predictor and does not provide for species effects on the rates per leaf mass. If leaf mass were used as the size index in scaling theory, many rates would be simply proportional (isometric). However, total plant mass is predicted to scale 4/3 with leaf mass and, conversely, many per-individual rates scale 3/4 with total plant mass [82]. Thus, the distinctive contribution of size-scaling theory is a series of predictions about conductive and supportive stem and root tissue mass as a 4/3 power of foliage mass. Flowing from these are also some allometric predictions about conductivities and sap velocities.

Size-scaling theory predicts ontogenetic change through the lifetime of individuals and does not predict differences between species for individuals at a common size. It should perhaps be thought of as complementary to ecological strategy differences between species, rather than as a dimension within ecological strategy theory.

was expected to trade off with resistance to embolism (the formation of gas bubbles in vessels, blocking the movement of water). Conductive efficiency was also expected to trade off with mechanical strength.

There are two mechanisms of embolism risk [31,32]. Under freeze–thaw, the risk that gas bubbles will form is proportional to vessel diameter. Under drought, gas bubbles are seeded through pores in the pit membranes, and wider pit-pores enable this to happen at less-negative xylem water potentials. Given these distinct mechanisms, one might think a species could simultaneously achieve very wide vessels and rapid conductance as well as narrow pit-pores and strong resistance to embolization under drought. Nevertheless, in Maherali *et al.*'s [33] compilation of data (167 species from 50 seed plant families; Figure 1), species with both fast water transport capacity and strong resistance to embolism were absent.

A probable reason why fast water-transport capacity is not found in combination with strong resistance to embolism is that resistances in the vessel lumen will have been coordinated by natural selection with resistances passing through walls between vessels. The overall conductivity of a stem is influenced not only by the density of lumens, but also by their size (conductance is proportional to the 4th power of diameter), by how often walls need to be passed through (vessel lengths) and by the resistance passing through each wall (number and size of pit-membrane pores). Measured conductances generally fall between 20% and 80% of the

theoretical conductance calculated from lumen diameters only [31]. Recently, Sperry *et al.* [34] showed by direct measurement that end walls and lumens contributed in roughly equal shares to the overall resistivity (inverse of conductivity); end walls contributed $54 \pm 7\%$ of resistivity across seven species with widely varying anatomies.

Wood density is a moderately good predictor of resistance to drought-driven embolism [32,35], measured as how low stem water potential can fall before 50% of conductance is lost. It might seem natural that wood density and resistance to embolism would be correlated, given that both can result from smaller vessels, and that vessels that go to lower water potentials need thicker walls to resist implosion [36]. Yet angiosperm wood anatomy provides many possibilities for weakening the relationship [36,37]. Fifty percent of conductivity can be contributed by a relatively few large vessels, because of the 4th-power-of-diameter effect. These larger vessels can occupy only a small share of the stem cross-section, with limited effect on wood density. The share of the cross-section that is not vessel lumen can vary in density. And as described here, drought-driven embolism is under the immediate control of pit-membrane pore diameters, rather than of vessel diameters. Nevertheless, Ackerly [38] and Bucci *et al.* [39] found higher wood density strongly associated with low leaf water potentials at the driest time of year across 20 California chaparral shrub species and six Brazil savanna tree species, respectively. These data indicated that species with higher wood density tended to be shallower rooted, or at least to be rooted in drier soil. It was consistent with wood density serving to protect conductivity in the face of falling xylem water potential.

Other than its relationship with hydraulic traits, higher wood density also incurs greater expense per stem volume and is connected to greater mechanical strength [40], slower tree growth rate [41–45], and (for reasons that are unclear) to smaller leaf size and twig size [38,46]. The conductive capacity of stems needs to be coordinated with the amount of leaf deployed and with the hydraulic properties of leaves [47]. Many species adjust leaf amounts over time in response to seasons and rainfall [48], but there are also continuing differences in leaf area per sapwood area across species along environmental gradients [49,50].

In summary, species vary in wood density, conductivity per unit cross-section of sapwood, leaf area per unit of cross section, and vulnerability to embolism. Higher wood density appears to be correlated with smaller leaf and twig sizes. It is not yet clear how many distinct dimensions of strategic variation are involved among these traits.

Roots in relation to shoots

First, one should consider the physiological or functional issues about root–shoot relations. Functional coordination is expected, because root-acquired resources are transferred to the shoot and vice versa. But does this mean that particular aboveground traits are always found in combination with particular belowground traits or,
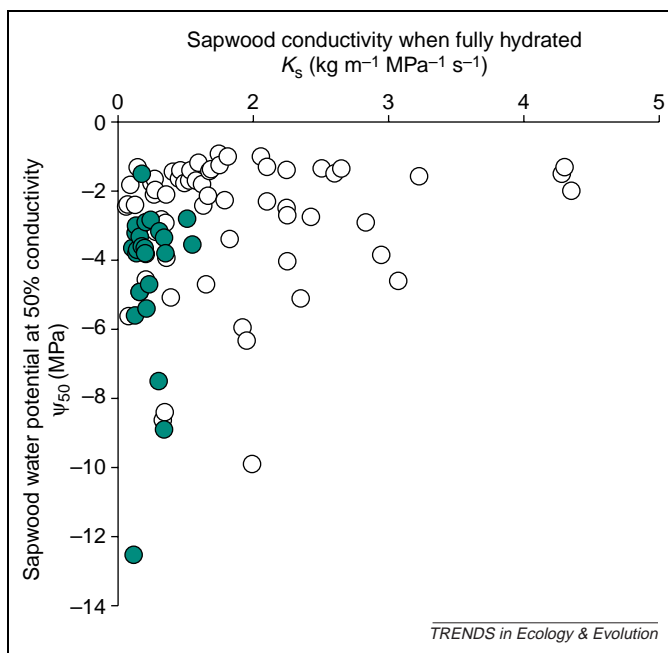
Figure 1. Cross-species tradeoff between specific conductivity of sapwood when fully hydrated (K_s) and vulnerability to cavitation measured as sapwood water potential at 50% conductivity (Ψ_{50}). A less negative Ψ_{50} represents greater vulnerability to cavitation. Results illustrate the absence of species having fast conductivity together with low vulnerability to cavitation but the presence of species having slow conductivity together with high vulnerability to cavitation. The resulting triangular relationship has weak *r* value of -0.31 (calculated on log-scaled data). The relationship across all species consists mainly of differences between major clades, especially with conifers (filled symbols) tending to have slower conductivity than angiosperms (open symbols). Data from [33], kindly provided by the authors.

alternatively, is there a wide variety of root traits cooperating with a particular type of aboveground plant? Second, roots are important for ecosystem outcomes under global change. The depth from which water is extracted is among the most important influences of vegetation on climate models. The metabolism of roots is a major unknown in carbon budgets, and root turnover is important for carbon storage [51].

At the level of the architecture of whole root and shoot systems, Schenk and Jackson's compilation of 1300 records worldwide showed that the stature of the plant was the dominant predictor of rooting depth [52]. Trees tended to have deeper roots than did shrubs, which tended to have deeper roots than did forbs and grasses. Within growth forms, species with larger aboveground volumes tended to have deeper roots and also wider lateral spread. However, there was much scatter, with r^2 values usually (0.5. Globally, deep-rooted species were most common in warm, high-rainfall, but seasonally dry environments, on soils that enable water to infiltrate deeply [53]. Still, half or more of all root biomass was found in the upper 30 cm of soil in all biomes.

Roots are hard work to excavate, and leaf water potential at the end of the dry season has been used as an indicator of rooting depth among 20 chaparral species [38]. It varied independently from leaf lifespan and other leaf-economic traits. Species with shallower roots (leaf water potential more strongly negative) tended to have higher wood density, smaller vessels, thinner twigs and less leaf area per sapwood area. Across 17 Florida oak species, those with higher wood density and slower conductivity similarly tended to carry less leaf area per sapwood area [54]. Low mid-day water potential in the dry season was similarly associated with higher wood density and slower conductivity sapwood across six tree species in Brazil [39] and 12 conifer species [55], but in these studies, leaf area per sapwood area was lower in the high-conductivity species.

At the level of individual absorbing roots, some traits of fine roots appear to be coordinated with traits of leaves. Among grasses on four continents, fine root N concentration was moderately well correlated with leaf N [56] (Figure 2), with C4 grasses operating at lower root N for a given leaf N than did C3 grasses. Across 31 North American savannah species from several growth forms, respiration rate increased with N concentration in leaves and roots, along a common relationship [57]. Leaf and root lifespan (14 species) decreased with tissue N concentration [57]. In a similar vein, Comas and Eissenstat [58] compared faster with slower growing temperate tree species within five separate clades, and found the faster growing species had narrower fine roots that achieved greater length for a given dry mass (i.e. greater specific root length; SRL).

In spite of these results, the picture about root trait–shoot trait relationships remains inconsistent. In Comas and Eissenstat's study [58], the faster growing species did not evince faster root respiration. In Tjoelker et al.'s study [57], leaf area per leaf mass (SLA=1/LMA) was not correlated with the SRL of fine roots (Spearman's ρ=0.12), although SLA and SRL had been previously been
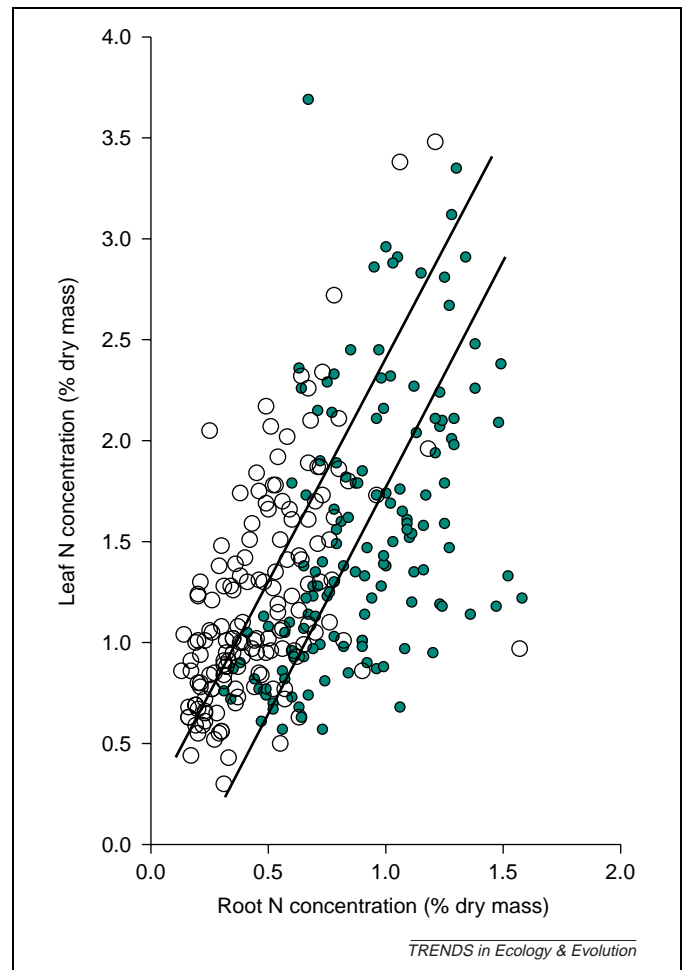
Figure 2. Correlation between leaf traits and fine root traits. Leaf N concentration in relation to fine root N concentration in C4 (open symbols) and C3 (filled symbols) grass species from Australia, South Africa, New Zealand and North America. Lines are standardized major axes. Data from [56], kindly provided by the authors.

correlated for seedlings in pots [59,60]. Wider comparisons are needed to put these studies in context.

N:P ratio in leaves, nutrient limitation and growth strategy

A leaf N:P ratio of ∼15 is thought to divide situations where growth responds more strongly to P addition (N:P>16) from situations where growth responds more strongly to N addition [61,62]. Recently, it has become evident that there is a strong gradient of leaf N:P increasing with mean annual temperature and towards the tropics [11,12,63,64] (Figure 3a). Discussion of possible causes for this revolves around the influence of temperature on soil weathering and on growth rate, P being used more heavily in protein synthesis, and N in photosynthesis. Still, individual species are scattered widely in leaf N:P at any given latitude or mean annual temperature (Figure 3b). What might this scatter mean?

Leaf N and P are strongly correlated, but with a log-log slope distinctly <1, estimated at 0.66 [10] or 0.75 [65] (e.g. Figure 3c). In other words, species with lower absolute N and P concentrations tend to have higher N:P ratios. On this basis, high N:P ratio should be associated with slow leaf-specific growth rates, as reported by Niklas et al. [65].
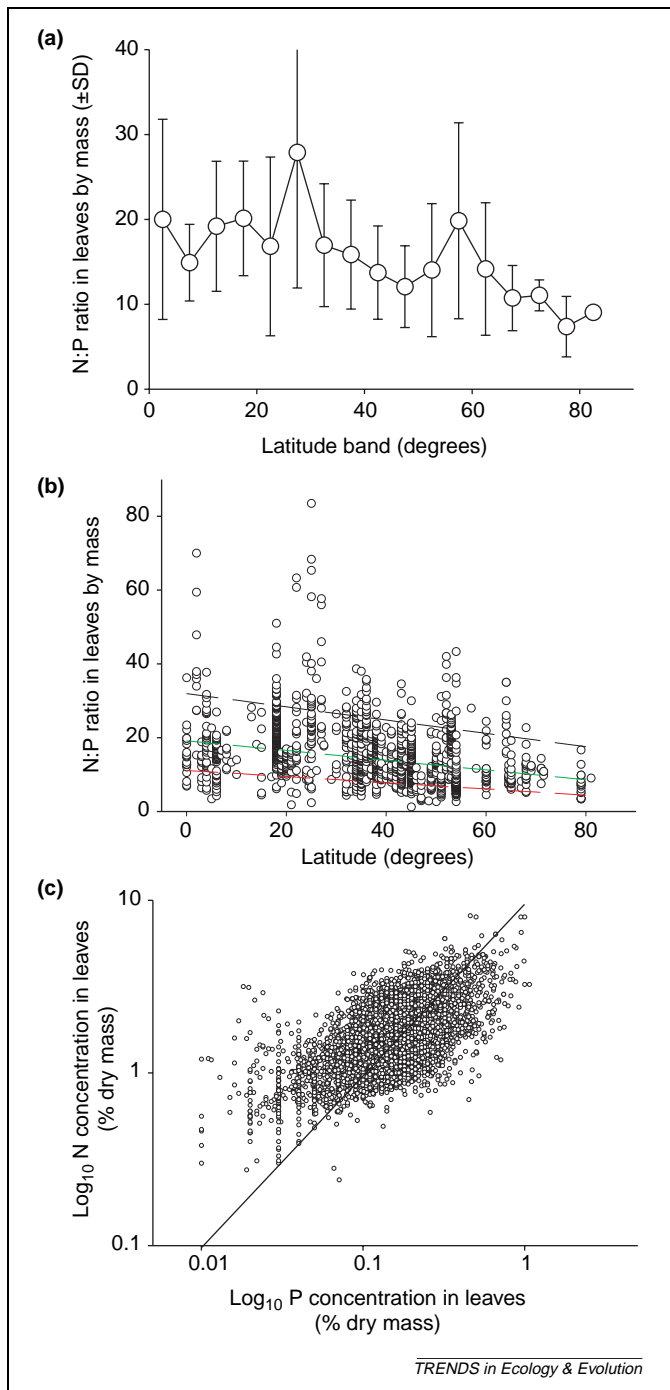
Figure 3. Patterns in leaf N:P relations across species. **(a)** Average leaf N:P ratio increasing towards the tropics in species grouped by the latitude bands in which they occur [12], $r^2 = 0.63$, $y = 2.25e^{-0.01x}$ **(b)** Leaf N:P ratio for individual species, showing wide variation at a given latitude. Broken lines are quantile regressions for 10th (red), 50th (green) and 90th (black) percentiles of the data. All three quantile regressions show significant trends, which demonstrates that the trend in the binned means is produced not only by the absence of the highest N:P ratios further away from the Equator, but also by a general shift in the distribution. **(c)** Log-log relationship between leaf N and P concentrations; $n = 7445$ from 1665 species. The SMA slope of this relationship is shallower than the 1.0 shown by the diagonal line, which means that species with higher overall nutrient concentrations tend towards lower N:P ratios, although with considerable scatter. Data from [12] (a) (b) and [65] (c), kindly provided by the authors.

This might account for much variation among species at a given site. Yet in a different data set, N:P ratio was only weakly correlated with elements of the leaf economic spectrum [66], and rarely within sites.

Conclusion

In reviewing plant traits, we have emphasized questions that remain unclear. We are however optimistic and expect the next 15 years to set in place a coherent understanding of Schimper world. The elements that need to come together are first, a strong grasp of trait costs and benefits, in the context of a competitive environment and expressed as quantitative models; second, worldwide trait data sets that can position each species in the context of the full spread of ecologies that has evolved; and third, a new generation of world vegetation models that will implement the cost–benefit models on real physical geography. These elements will add up to a major consolidation of ecological science, with a wide range of practical applications.

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