Research Focus

Challenges to the generality of WBE theory

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The West, Brown and Enquist (WBE) theory has attracted great interest because it makes general predictions about scaling of ecological processes with body size. Recent research by Muller-Landau and co-workers challenges the generality of this theory by showing that demographic processes in natural forests do not scale in the way that the theory predicts. For WBE theory to be relevant to plant community dynamics, more complex models are required to deal with the influences of competition for light, nutrient supply and disturbance experienced by such communities.

What is WBE theory?

There is nothing like a new theory of everything to get researchers talking, and the arrival of such a theory at ecology's doorstep has been greeted with a predictable mixture of hype and hostility. West, Brown and Enquist (WBE) have caused something of a stir by claiming to have discovered general laws of ecology, derived from first principles [1–4]. The theory consists of several related predictions contained in a series of papers. At the foundation of WBE theory are ideas about the optimal design of vascular systems [1] (Box 1). Later publications move on to consider how the vascular architecture of plants affects whole-plant physiology, population dynamics and community ecology (Box 2) [2–4]. These theories are persuasively presented because they are supported by numerous pieces of empirical evidence.

Testing predictions about forest growth

Two recent papers by Muller-Landau and co-authors have challenged the generality of the WBE theory when applied to natural forest communities [5,6]. According to WBE theory, stem diameter growth (dD/dt) should scale with $D^{1/3}$, where D is stem diameter, and this relationship should apply universally (Box 2). By analysing long-term data collected from ten large plots located across the tropics, Muller-Landau *et al.* tested whether this theory applied to trees growing naturally in tropical forests [5]. These plots contain a total of 1.7 million trees, all of which have been tagged and monitored for diameter growth for about a decade. The authors constructed size-specific growth curves from these data (e.g. Figure 1) and then fitted power functions to these curves. Their results amount to a firm rejection of the WBE theory: the scaling exponents deviated significantly from 1/3 in nine of the ten sites, and were found to vary considerably among sites (from −0.27 to 0.75).

So why does the growth model fail in tropical forests? One of the assumptions of WBE theory is that all leaves within a forest canopy photosynthesise at the same rate (Box 2); however, this is inadequate in natural forests because it does not account for the strong vertical gradient in light within a canopy and its probable influence on photosynthesis rates. Understories are usually deeply shaded, whereas the canopy is usually bathed in intense sunlight in which much of the activity of the forest seems to happen. Muller-Landau *et al.* quantified the light gradient in Panamanian forests by measuring canopy openness along a vertical profile, and found that it increased by almost 100-fold between 1- and 30-m height [5]. They argued that light limitation is as important as hydraulic constraints in determining the scaling of growth with tree size in natural forests, because small trees are out-competed by their taller neighbours in the battle to capture light and consequently grow slowly. Thus, although WBE theory might apply to trees growing in isolation, competition for light also influences the growth of trees in tropical forests [5].

Tree size distributions

The second paper by Muller-Landau and colleagues [6] challenges the proposition of Enquist and Niklas that the tree size distribution of natural mixed-aged forests is a function of D^{-2} [4]. This prediction was tested by fitting curves to the diameter distributions of trees in 14 tropical forest plots. The results from Sri Lanka are typical of the general result (Figure 1c): for small trees, the size-density data fall along a straight line on log–log axes, indicating that a power function is appropriate for describing this distribution, but when all trees are considered, the power function is inadequate because fewer large trees occur than predicted. The scaling exponents were significantly different from −2 at most of the 14 sites.

What might have caused these discrepancies between theory and reality? One explanation is that Enquist and Niklas make an untenable assumption when they derive their theory of size distributions within natural mixed-aged forests [4] from previous work on self-thinning in even-aged forests [2]. The assumption for self-thinning stands is that leaf area remains constant throughout stand development [4,8], and that all stands receive (and use) the same amount of energy as a consequence. This leads to prediction that stem density scales with D^{-2} (Box 2). When extending this theory to natural forests, the authors assumed that different size classes within a stand would receive (and use) the same amount of energy, from which they deduced that the same thinning rule should apply in mixed-aged forests as in even-aged stands. However, there

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An unavoidable consequence of photosynthesis is that water is lost through open stoma; leaves must replenish that water by transporting sap over long distances via the vascular system, which consists of specialized cells that interconnect to form pipes. These pipes are extremely narrow at the point of delivery as they have to deliver water into the leaf lamina. This creates a problem, because such narrow pipes are inefficient at delivering large volumes of water; resistance scales as the quarter power of diameter, so halving the diameter of pipe causes a 16-fold reduction in flow rate.

WBE propose that plants have evolved optimally efficient vascular systems by having slightly wider pipes in their trunks than in their peripheral branches and leaves. Assuming that the branching architecture of trees conforms to volume-filling fractals, WBE theory predicts that pipe diameter d_i at level i of the branching system scales with the stem diameter D_i raised to 1/6 [7] (Figure I). Recent studies of wood anatomy have reported scaling functions similar to the one predicted, even though some of the assumptions of the WBE model are unrealistic, such as the suggestion that volume-filling fractals equate with actual branching patterns [7].
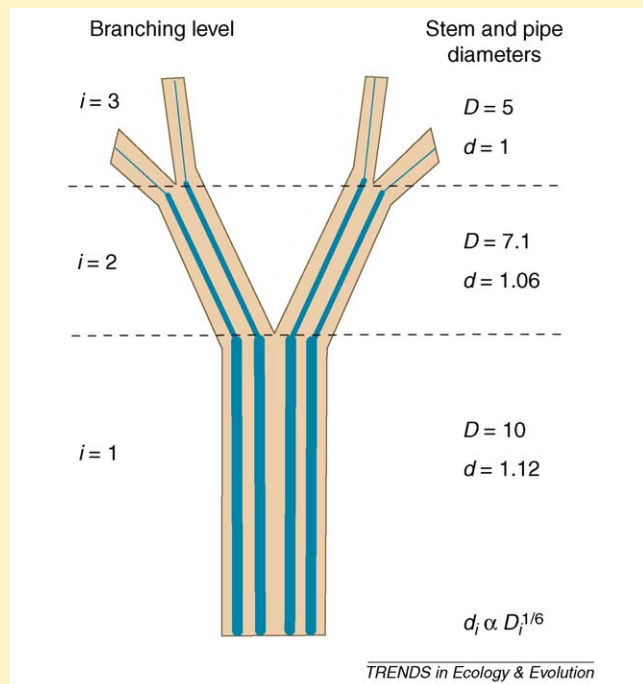

Figure I.

is no *a priori* reason for making this assumption: indeed the strong vertical light gradient found in forests suggests that equal partitioning of energy is unlikely [6].

Muller-Landau *et al.* explored this issue using demographic modelling [6]. The size distribution of a forest is a property that emerges from individual demographics and, provided that a system is in dynamic equilibrium, can be estimated from size-specific growth and mortality curves [8]. The authors found that size distributions estimated from growth and mortality curves were similar to the actual distributions observed in tropical forests, and generally had a form similar to a Weibull distribution.

Muller-Landau and colleagues also explored the types of size distribution produced by various growth and mortality curves [6]. For example, they showed that diameter distribution takes the form of a negative exponential distribution if growth and mortality remain constant with size, but has a Weibull-like distribution if growth and mortality are both power functions of diameter. Because diameter growth did not scale with $D^{1/3}$ in any of the tropical forests examined, they showed that it was mathematically inevitable that the size distributions could not scale with D^{-2}. The implication is that uneven partitioning of energy (i.e. light) within forest canopies affects the growth rates of trees and, consequently, violates the assumption made by Enquist and Niklas [5].

Another problem with Enquist and Niklas theory is that it predicts mortality to decline steadily with size (Box 2), but the situation in real forests is more complex because large trees are often observed to have high mortality rates, perhaps because they are exposed to strong winds, or are weakened by age [8]. As a consequence, mortality curves are often observed to be U-shaped (Figure 1b). The predisposition of large trees to disturbance and senescence might explain their dearth within the forests studied (Figure 1c).

The relatively weak influence of hydraulic limitation on community processes

Metabolic theory is described by its creators as 'a model that invokes the minimum possible assumptions necessary to derive the scaling relationships of interest' and it is
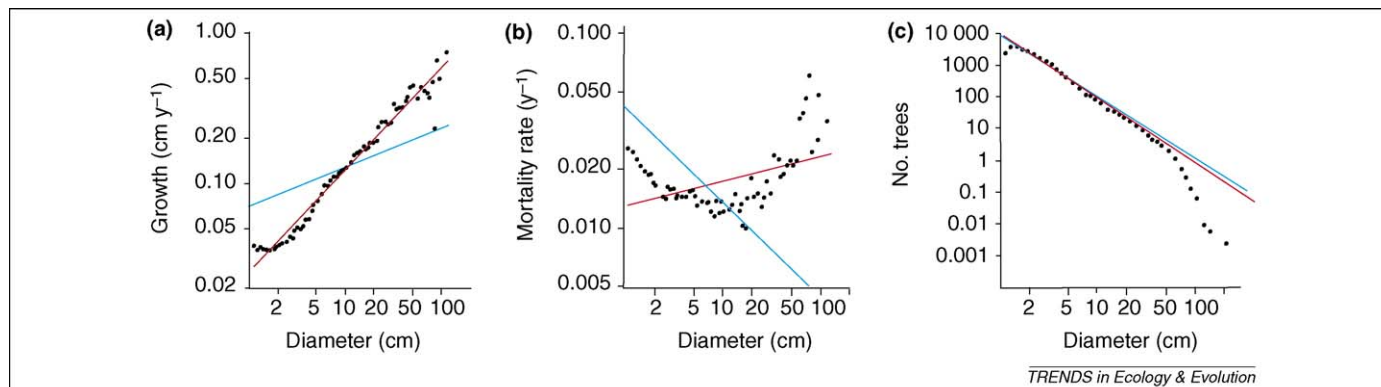

Figure 1. The scaling of growth **(a)**, mortality **(b)** and stem density **(c)** with stem diameter, determined for 171 000 trees within 25 ha of tropical rain forest in Sri Lanka. All axes are on the log scale. Power functions fitted to the growth and mortality data (in red) deviated substantially from those predicted by WBE theory (in blue), whereas the function fitted to the stem density data was similar to the theoretical curve, but had fewer large trees than predicted.

Box 2. An overview of the WBE theory of plant metabolism

Growth and allometry

Optimized vascular systems, as envisioned by WBE are extraordinary in that the hydraulic resistance within a pipe is independent of its length [1–3]. Consequently, the photosynthetic rate of leaves should remain constant as a tree grows, because the transport system continues to supply water at the same rate. The carbon assimilation rate of a whole tree is calculated by integrating the photosynthetic rate (P) of its leaves. This calculation is straightforward when all the leaves are photosynthesising at the same rate: it is simply the leaf area of the tree A multiplied by P. Therefore, this chain of logic leads to the prediction that the assimilation rate of a tree is directly proportional to A.

WBE use these ideas to predict the way in which biomass growth (dM/dt) scales with A, by assuming that a constant proportion of assimilate is respired and the remainder is used to build new tissues. Other growth relationships can now be derived, because A, stem diameter (D), height (H) and biomass (M) are all interrelated by allometric relationships [3]; thus, they can be interchanged within the same fundamental scaling rule. For instance, A is predicted to scale with D^2 based on the 'area-preserving branching' rule of Leonardo da Vinci, and H is predicted to scale with $D^{2/3}$ because this represents the limits of height before a tree becomes structurally unstable. It is also predicted that M scales with $D^{8/3}$. These allometric relationships enable the size dependence of growth to be represented in several ways (Figure Ia).

Mortality and stem size distributions

WBE theory assumes that plant populations maintain a constant leaf area (per unit ground area) during stand development (Figure Ib). This packing rule implies that as A of individual trees increases during stand development, the total leaf area (LAI) remains constant and the stem density (N) falls, that is: $N \times A = LAI$ = constant, from which it follows that N scales with A^{-1} or, equivalently, with D^{-2} [2], and that mortality scales with $D^{-2/3}$ (Figure Ib) [6].

Table I consolidates these interconnected theories by following the development of a tree population over four successive time steps. A tree grows two new branches each time step from each branch present in the previous time step, so that A doubles. Allometric relationships determine the way in which D, H and M vary with the expansion in A (these are expressed as a proportion of their values in the first time step). The LAI remains constant during stand development, whereas N declines. The total biomass M_T of a stand increases over time, but its productivity dM_T/dt remains constant.
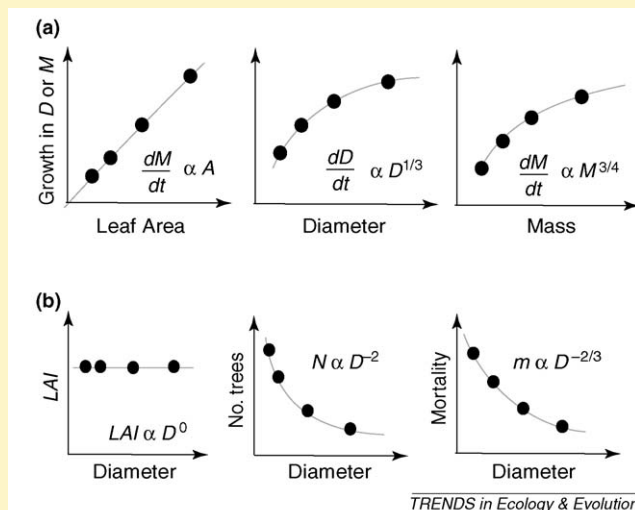
Figure I.

Table I. Stand development in even-aged forests

Per tree				
Leaf area (A)	1	2	4	8
Diameter (D)	1	1.4	2	2.8
Biomass (M)	1	2.5	6.3	16
Growth (dM/dt)	1	2	4	8
Per unit ground area				
No. trees (N)	8	4	2	1
Leaf area (LAI)	8	8	8	8
Biomass (M_T)	8	10	12.6	16
Growth (dM_T/dt)	8	8	8	8

freely acknowledged that these assumptions are 'zeroth-order approximations' [1]. Some refinements might make relatively little difference to the predictions of the model. For instance, assuming that a tree produces branches that occupy a plane rather than fill a volume might only lead to subtly different predictions about the relationship between pipe-size and stem size. However, the work of Muller-Landau and colleagues highlights that including competition for light and disturbance into the model results in fundamentally different predictions about the scaling of demographic processes with size [5–6,8].

Building realistic nutrient dynamics into WBE theory could also result in profoundly different predictions, as Reich et al. have shown [9]. They found that whole-tree respiration rate was linearly related to whole-tree nitrogen content, which makes good sense because nitrogen is a major constituent of all enzymes involved in metabolism. However, the respiration rate of these trees did not scale as a three-quarters power of biomass, as WBE theory predicts (Box 2). Reich *et al.* point out that the nitrogen content of a plant is not necessarily correlated with the supply of nutrients via the transpiration stream,

because plants recycle a large proportion of nutrients from senescing tissues, so stocks are partially decoupled from supply. Therefore, the scaling of nitrogen stocks is a complex issue.

Concluding remarks

Most evidence in support of WBE theory comes from comparisons of plants of vastly different sizes [1–3], but it does not accurately predict what happens within populations of trees within forests [5,6,8,9]. The distinction is important as the realities of light limitation, competition for nutrients, disturbance and other drivers apparently swamp out the potentially real effects that WBE theory might encapsulate [10]. Therefore, developing a more sophisticated theory to predict community-level processes remains a complex, yet tantalising, challenge.

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