

Alternative Designs and the Evolution of Functional Diversity

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Submitted February 28, 2005; Accepted August 5, 2005;
Electronically published October 11, 2005

Online enhancement: table.

ABSTRACT: According to conventional wisdom, functional diversity is exclusively a consequence of species having evolved adaptations to fill different niches within a heterogeneous environment. This view anticipates only one optimal combination of trait values in a given environment, but it is also conceivable that alternative designs of equal fitness in the same environment might evolve. To investigate that possibility, we use a genetic algorithm to search for optimal combinations of 34 functional traits in a realistic model of tree seedling growth and survival. We show that separate lineages of seedlings evolving in identical environments result in many alternative functional designs of approximately equal fitness.

Keywords: alternative designs, convergent evolution, functional diversity, niche overlap, trait adaptation, tree seedlings.

One of the most striking observations from tropical lowland rain forests to boreal conifer forests is the high levels of quantitative variation in traits among co-occurring tree species. The within-site variation among species in the value of traits critical to plant function usually exceeds an order of magnitude (Niinemets 2001; Maherali et al. 2004; Wright et al. 2004) and can be greater than among-site variation (Westoby et al. 2002). This observation raises the question of why the values of traits have not converged to a greater degree in species that are currently growing in the same environment (Körner 1991). Here we show that in evolution, a set of traits can be combined in quantitatively different ways to achieve approximately equal fitness in a given environment, which can account for the observed functional diversity among co-occurring trees in

contemporary forests. Furthermore, we show that this mechanism is a general one that could contribute to the evolution of functional diversity in all types of organisms.

The traditional view of trait evolution holds that selection favors individuals well suited to their environment, individuals with traits and trait combinations that increase fitness. For tree seedlings, fitness can be assumed to be the combination of survival and maximization of growth. Maximizing seedling growth increases the chance to survive into adulthood and increases lifetime reproductive potential (Van Valen 1975; Harcombe 1987; Oliver and Larson 1996). Growth and survival are in turn a function of the resource balances of the seedling, particularly light (Pacala et al. 1994), carbon (Kobe 1997), water (Caspersen and Kobe 2001), and nutrients (Aerts and Chapin 2000). Traits should evolve toward values that improve these resource balances and thus growth rate in a given environment (Parker and Maynard Smith 1990; Mäkelä et al. 2002).

This view has been formalized in various mathematical optimization models (Parker and Maynard Smith 1990; Mäkelä et al. 2002; Sutherland 2005). Typically, these models focus on a single trade-off that governs a particular trait of interest. We refer to this class of models as single trade-off models. A trade-off is described by both costs and benefits that vary in some nonlinear fashion with the value of the trait. Consequently, there is usually a single optimal trait value that maximizes fitness. If the equations modeling these costs and benefits are cleverly chosen, then it is often possible to solve for the optimal trait value analytically, which has made these models enticing. We will not elaborate an explanation of single trade-off models; the approach is reviewed elsewhere (Parker and Maynard Smith 1990; Mäkelä et al. 2002). The key point here is the contradictory observation that single trade-off models predict a single optimal trait value in a particular environment, yet field researchers consistently measure great variation in trait values among tree species at a given site (Niinemets 2001; Westoby et al. 2002; Maherali et al. 2004; Wright et al. 2004).

How can the prediction of the single optimal trait value be reconciled with the great variation observed in the field? The standard ecological explanation is that the field site

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must be heterogeneous (in either time or space) and thus does not represent a single environment but rather a complex of microenvironments or a series of fluctuating environments, each selecting for different optimal trait values (Levin and Muller-Landau 2000). These explanations include not only the abiotic environmental heterogeneity but also the environmental heterogeneity imposed by the organisms occupying the environment (e.g., Iwasa et al. 1984). However, it seems doubtful to us that the relatively minor environmental variation within a site could explain all of the large trait variation observed in co-occurring plant species, especially given the typically low correlation between trait values and environmental variables (Niinemets 2001; Maherali et al. 2004; Wright et al. 2004).

The propensity of trees to be habitat generalists casts further doubt on local heterogeneity as the explanation for functional diversity at a site. For example, ecologists are discovering that in the diverse forests of the wet tropics, most tree species are habitat generalists (Ricklefs 2000; Pitman et al. 2001; Valencia et al. 2004). This implies frequent niche overlap in these species despite great trait diversity. Even in the less diverse temperate forests, many species are generalists (Burns and Honkala 1990), and in-depth studies of tree species distributions on environmental gradients have shown large overlap in niches (Whittaker 1956; Fralish et al. 1978; Iverson et al. 1999; Cavender-Bares et al. 2004a). In fact, this niche overlap is so great that it has led some researchers to propose that niche differences can be neglected in neutral models of community assembly (Bell 2000; Hubbell 2001, 2005).

We recognize the importance of environmental gradients and niche partitioning in promoting diversity, especially in the radiation of a single lineage (Schluter 2000; Cavender-Bares et al. 2004b). However, the ecological patterns discussed above cast substantial doubt on environmental heterogeneity as the sole explanation for the variation in plant traits encountered within a locality for species from diverse lineages. As an alternative, we propose that if a model of tree seedling growth and survival were based on the complex interactions among multiple trade-offs instead of a single trade-off, then multiple optima could emerge even in a single environment. Multiple optima imply that diverse trait combinations are feasible in the same habitat, each representing an alternative functional design of approximately equal competence. Because of the effects of history and chance, different lineages would be expected to evolve toward different optima (Bock 1959, 1976, 1980; Lewontin 1978; Gould 1989). For example, it is conceivable that a red oak-type design and a white oak-type design may be equally well adapted to the same habitat despite substantial trait differences (Cavender-Bares et al. 2004b).

We have a high regard for the elegance of single trade-

off models and the interesting insights that can be gained from such models. However, it is important to recognize that single trade-off models isolate some part of plant function and thereby limit the possibilities for adaptation at the whole-plant level (Gould and Lewontin 1979; Mayr 1983). In real organisms and especially in plants, traits often have a critical role in more than a single function, and trait values therefore reflect the outcome of trade-offs among functions that are not readily assessed in a single trade-off model. More holistic models that explicitly consider the many trait interactions governing function allow us to better explore the consequences of this complexity at the whole-plant level (Ellis 2005; Proulx et al. 2005). Specifically, in this article, we take a holistic approach to test the hypothesis that the complex interactions among multiple traits result in the existence of alternative, more or less equally competent functional designs in a given environment. We present the existence of alternative, equally competent functional designs as a likely mechanism that can account for the high levels of trait variation in tree species with similar habitat affinities. Our simulation results provide a novel explanation of how the functional diversity among tree species observed in a locality might have evolved and offer some indication of the degree of functional redundancy inherent in species diversity.

Model

To test our hypothesis, we developed a simulation model of tree seedling growth and survival combined with a genetic algorithm (GA) to search for optimal trait combinations. We describe this tree seedling adaptive design model (TAD) in detail elsewhere (Marks and Lechowicz, forthcoming) but outline the model here to support our consideration of alternative functional designs.

Seedling Simulation Model

The TAD model is based on the interactions and particularly the trade-offs among 34 key functional traits. The resources considered in the modeled trade-offs include light, carbon, water, and nitrogen. We refer to the 34 trait variables that are subject to optimization in the model as independent traits, whereas other traits that are derived from these independent traits are referred to as dependent traits. Consideration of the trade-offs among this relatively large number of traits has several advantages. First, it allows testing the hypothesis that multiple optima for a given environment can result from the complex interactions among multiple traits. Second, interactions among the traits can be integrated at the whole-seedling level to give a single realistic fitness measure (i.e., survival and growth rate). Finally, the rich array of interacting traits increases

the realism of the simulated seedlings and lets the key traits and derived traits be compared with reported data for natural seedlings in diverse environments.

The 34 traits were selected after a thorough review of the literature on the functional ecology of woody plants. The primary criterion for letting a trait be an independent variable in the model was that the trait has a substantial and well enough understood effect on one or more trade-offs involving resource balances to model accurately. Because leaves have been studied more intensively than roots, the model has a more detailed representation of above-ground than below-ground traits, but many below-ground traits and processes are included. The 34 independent traits include four parameters related to seed reserve allocation, six parameters related to carbon allocation, three parameters involved in nitrogen allocation, three parameters for stomatal control, nine leaf traits, five root traits, and four wood traits.

The essence of the TAD model is the ensemble of functional trade-offs and their interactions. We introduce the modeled trade-offs in the following paragraphs to give the reader some insight into their complexity. We present elsewhere a more detailed description and validation of the model, including equations defining the functional trade-offs and trait interactions together with a supporting literature review (Marks and Lechowicz, forthcoming). The brief summary of the model here is intended to be didactic and omits supporting references and details to emphasize the overall nature of the TAD model.

Leaves use all four modeled resources (light, carbon, water, and nitrogen), making the interactions among leaf traits particularly complex. For example, leaves have stomatal pores to regulate gas exchange with the surrounding air. Increasing stomatal conductance allows more CO₂ to diffuse into the leaf, thereby increasing the photosynthetic rate, but at the same time increases the amount of water lost from the leaf through transpiration. Because supplying the leaf with water is costly, particularly in dry environments, a plant should regulate its stomatal conductance such that it maximizes photosynthesis relative to transpiration. Similarly, leaves have a cuticle to reduce water losses. Investing in a thicker cuticle improves survival during a prolonged drought but also increases leaf construction cost. Thus, there are multiple trade-offs between the carbon and water economy in leaves.

The numbers of mesophyll cell layers in leaves, and consequently leaf thickness, may vary. More layers increase the total photosynthetic capacity of the leaf, but upper layers will shade lower layers, preventing them from getting sufficient light for photosynthesis, especially under low-light conditions. Because leaf transpirational losses are proportional to surface area, the number of mesophyll cell layers also affects the ratio of photosynthesis to transpi-

ration (or water use efficiency), thus creating a link between trade-offs related to light and water. The mesophyll cells of the leaves may contain more chloroplasts to increase their photosynthetic capacity, but this is also associated with a greater nitrogen investment and greater maintenance respiration rate. Thus, there are also a number of trade-offs of the nitrogen and light economies with the carbon and water economy of the leaf.

The thickness of leaf cell walls relative to cell diameter limits the maximum pressure that the cell wall can resist without rupturing. Increasing cell wall thickness or decreasing cell diameter can increase the maximum allowable osmotic potential of leaf cells, which is critical to the plant's ability to draw in water at low soil moisture. However, thicker cell walls not only have a greater construction cost but also increase shading of mesophyll cells. Similarly, increasing leaf cell diameter decreases internal shading but also decreases the surface-area-to-volume ratio of the cell and thus reduces the internal conductance to CO₂ diffusion and thereby reduces photosynthetic rate. Thus, there are trade-offs between the ability to survive drought and the resource economies of the leaf.

Leaves may contain varying amounts of sclerenchyma. Sclerenchyma increases the strength of a leaf. Similarly, the thickness of mesophyll cell walls relative to mesophyll cell diameter increases the strength of the leaf at the cost of increased carbon investment. In general, the longevity of leaves is a function of their strength, presumably to resist mechanical damage by herbivores or wear and tear from wind. Trees also can invest in petioles, the rachis of compound leaves or twigs, to display their leaves. A deciduous petiole or rachis is less expensive to construct, whereas twigs may be reused to support new leaves after the old leaves senesce. There is a general trade-off between tissue construction cost and longevity.

The complex system of trade-offs for leaves is functionally linked with the trade-offs among the traits of the support structures such as the stem, branches, and thick roots. These support structures supply the leaves with the resources they need in exchange for carbon fixed in the leaves. For example, a higher hydraulic conductance increases water supply to the leaves, which allows higher transpiration rates and consequently higher photosynthetic rates. The total stem or branch cross-sectional area affects this hydraulic conductance but also increases construction cost of the structure. Furthermore, xylem conduits that can withstand lower water potentials to survive droughts need to have thicker cell walls to guard against implosion in the case of cavitation, and this increases investment costs per conduit. The relative thickness of the conduit walls determines wood density and thereby wood strength. There is a direct link between the hydraulic and mechanical traits of the wood. In particular, stems can be

extended in height and crowns can be extended in width to intercept more light, but as stems and branches become longer, their construction and maintenance costs also increase, as does the load that needs to be supported mechanically by the stem. To support this increasing mechanical load, the stems and branches must increase in cross-sectional area, further increasing construction and maintenance costs. Thus, in stems, there are three-way trade-offs among the economies of light, carbon, and water, as well as interactions with leaf traits.

As in leaves, in fine roots, there are trade-offs among resource uptake, nitrogen investment, and maintenance costs. For instance, fine roots can have a greater investment in metabolic activity associated with higher nitrogen content and higher nutrient uptake rates, but this increases their maintenance respiration and construction costs. Furthermore, fine roots can be distributed primarily in the upper soil layers, where nutrients are most abundant but where evaporation is also greater, or in deeper soil layers, where they can avoid competition and moisture availability is typically greater, but then the length of coarse roots must increase. Thus, there is a three-way trade-off among nutrient uptake, water uptake, and root construction costs.

These diverse trade-offs among traits within an organ type also interact with each other indirectly at the level of the whole seedling through the overall carbon, nitrogen, and water balances. Because these resource balances determine the seedling's growth and survival, it is clear that the relationship between any one individual trait and fitness is very complex, with numerous direct as well as indirect effects. The inclusion of these indirect effects is an important advantage of the multi-trade-off model approach over single trade-off models.

Genetic Algorithm

Given the complexity of the interactions and trade-offs among traits in the TAD model, we required a powerful numerical technique to find optimal solutions. We wrote a GA for this purpose (Marks and Lechowicz, forthcoming) on the basis of the recommendations for mathematical efficiency given by Goldberg (1989). GAs are numerical optimization techniques initially developed in analogy to biological evolution (Goldberg 1989). They are not an accurate representation of actual biological evolution, although qualitatively they may display many of the same behaviors and constraints on evolvability (Wagner and Altenberg 1996). For example, our algorithm considers a population of seedling designs evolving via mutation, recombination, and selection, but population size and mutation rate are set for mathematical efficiency, not for biological realism. Our GA is only a powerful numerical

technique to find possible optima within the potential trait combinations in the TAD model.

Simulations

To test our alternative design hypothesis, we ran the GA 100 times to search for optimal trait combinations, each time starting with a different random trait combination. Our optimality criterion required first that a seedling be mechanically sound and able to survive in the test environment and then that seedling growth over a simulated period be maximized (Marks and Lechowicz, forthcoming). Each of the 100 replicate runs involved 2,000 cycles generating variants and selecting among them to insure that the algorithm had stabilized on an optimum combination of tree seedling trait values, which we will refer to as a design.

The TAD model can explore alternative designs in a wide variety of test environments, but all the simulations reported here were run under the same environmental conditions. Seedling growth was simulated for 250 days, with a loam soil, humid air, and high light, under a warm climate. Soil water was replenished to 95% of field capacity over the entire soil profile every 30 days. The nitrate input to the soil was at a rate of 10 g N/m²/yr, typical of a fertile forest site (Larcher 2003), and the atmospheric CO₂ concentration was 355 ppm, a representative modern ambient. The simulated environment did not include competing neighbors, and thus the results correspond to an open-grown tree seedling. The choice of these relatively benign environmental conditions for the simulations may seem arbitrary, but subsequent simulations under a variety of different conditions including more stressful environments led to the same broad conclusions, even when neighbor-neighbor competition was included (C. O. Marks, unpublished manuscript).

Results

Each of the 100 simulations found a different optimal combination of trait values representing a viable, alternative tree seedling design in the test environment. We computed the fitness of a design as the simulated growth and survival of that variant design. If a seedling of a particular design survived and did not fail mechanically during the 250-day simulation, then its fitness is its final dry mass; otherwise, its fitness is 0. Because the simulation time was always 250 days, final dry mass is directly correlated to average growth rate, a widely accepted measure of tree seedling fitness. A rank order diagram of fitness for the 100 designs (fig. 1) indicates that not all the designs capable of surviving in the test environment have the same fitness. In other words, the optima found by the GA are

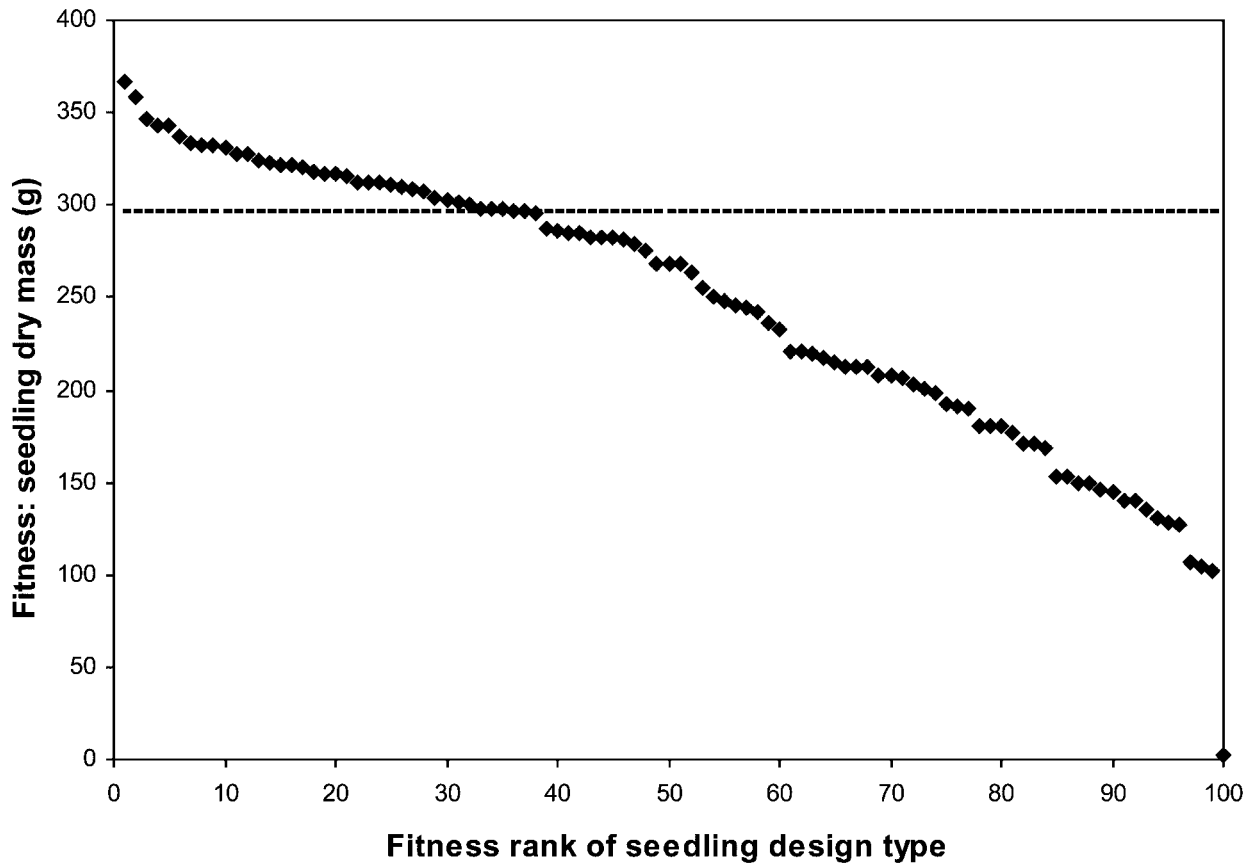


Figure 1: Fitness (seedling dry mass after a 250-day growing period) for the 100 seedling designs where each design represents an optimal combination of trait values found by the genetic algorithm in a simulated growing season. The horizontal line indicates where fitness is 20% lower than the fitness of the best design. Of the 100 designs, 37 are above this line. We focus on these top 37 designs because they could be considered both well adapted and approximately equivalent in fitness.

local optima within the trait space, not necessarily global optima. Despite this range in fitness, a substantial set of these locally optimal designs converges to a similarly high level of fitness in the test environment. For example, 37 of the 100 designs had a fitness that was within 20% of the maximum (fig. 1). Because our hypothesis is concerned with the evolution of alternative designs that are approximately equally fit in terms of seedling growth and we consider the designs that were not within the top 20% to be relatively poorly adapted in this regard, we restrict our subsequent analyses to only these 37 best designs among the 100 locally optimal designs.

To determine whether the diverse seedling designs found by the GA are indeed representative of truly alternative designs rather than slightly different versions of the same general design, we examined the variation in their trait values. We used a cluster tree based on similarity in trait

values to summarize and assess the patterns in overall trait variation among the top 37 designs (fig. 2). If evolution in the model were converging on a single optimal design, one would expect the designs with the highest fitness to form a group in the cluster tree, but this is not the case (fig. 2). This point can be made more explicit by plotting the fitness difference between design types versus the distance they are apart in the cluster tree (fig. 3). If there were convergence, the plot would show a positive relationship, which it clearly does not. These results imply that quite comparable fitness can be achieved in substantially different ways. For example, 23 out of the 34 independent traits differed by a factor of two or more, and only three traits had converged completely in the five most-fit designs. It is important to remember that all 34 traits contribute to the fitness of a design. Consequently, trait variation is representative of differences among optima, not

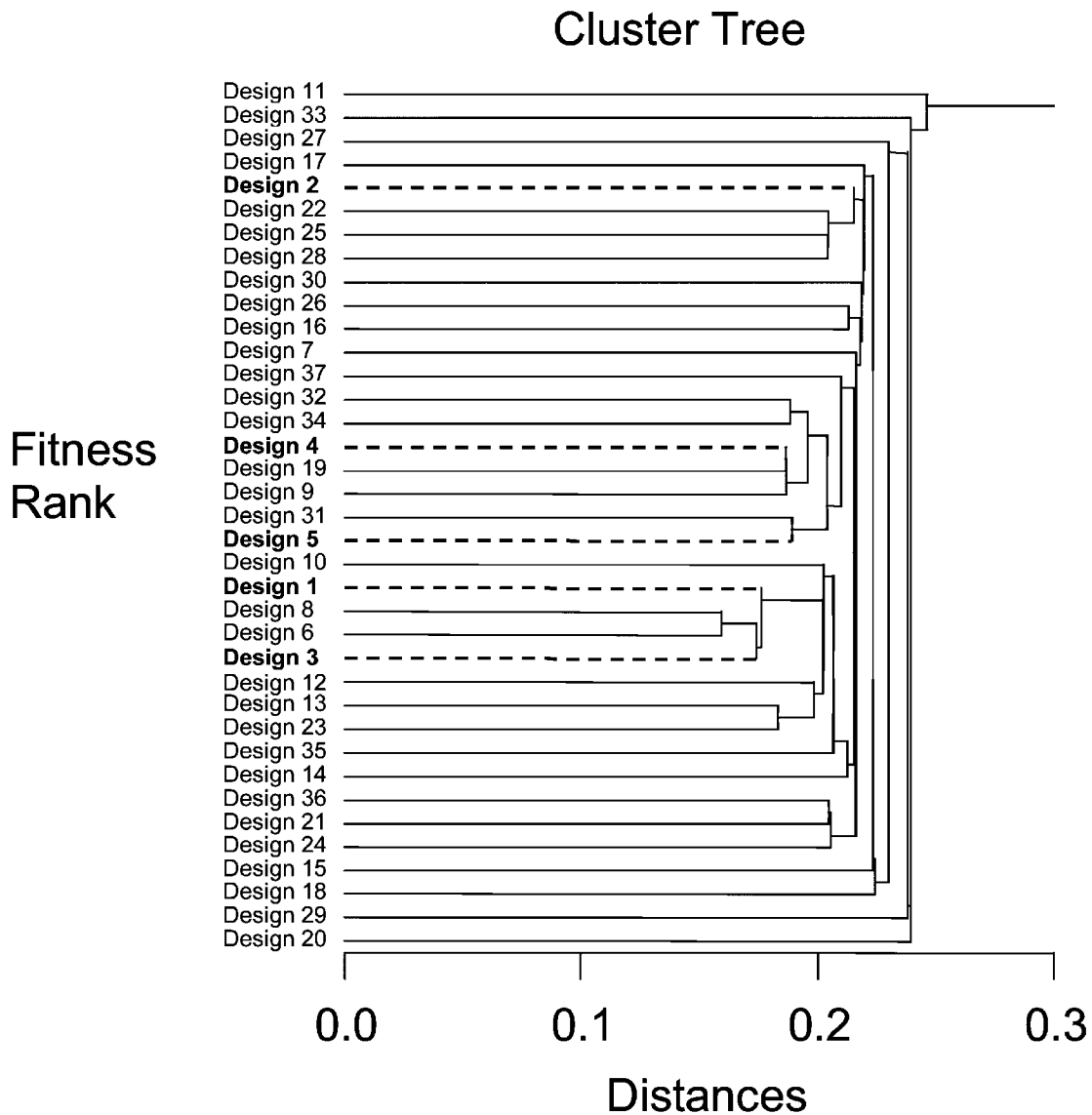


Figure 2: Cluster tree using simple Euclidean distance and single linkage to compare similarity in the 34 independent traits among the optimal tree seedling designs (SPSS 1998). Each case represents an optimal design, where the design number represents the rank of that design in terms of fitness. The values of the 34 independent traits were normalized by the maximum value in the range of possible values for that trait to insure that all traits are weighted equally in the cluster tree. Only the 37 best seedling designs (i.e., fitness within the top 20%) were included in the analysis because the focus of the project is on alternative designs that are approximately equally well adapted. For example, note that the five highest-ranked designs are not all located in the same cluster within the tree. If the results were converging on a single optimal design, one would expect the five best designs to be located in the same cluster. We highlighted these five designs in the tree by using dashed lines.

as a result of drift in selectively neutral traits. The large variation in trait values from design to design indicates that not only do the optima represent distinct functional designs but also these alternative designs are located far apart in trait space.

Although the model does not need to be a very accurate description of tree seedlings to answer our primary ques-

tion, the results are more interesting and convincing if it can be shown that the optimal seedlings are reasonably realistic. We found several statistically significant bivariate relationships between dependent leaf traits (table 1) that compare well with relationships reported in the literature. In particular, the globally valid relationships among leaf mass per area, mass-based leaf nitrogen content, and max-

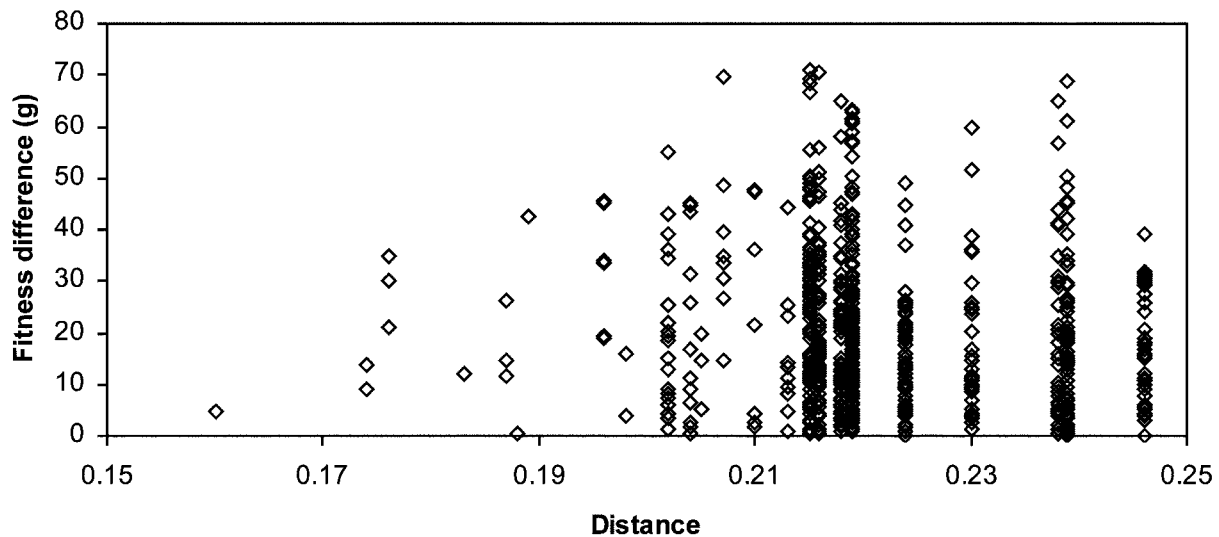


Figure 3: Plot of fitness difference between the designs in figure 2 versus the distance measure of their trait similarity from the cluster tree. If the designs were converging on a single design type, a significant positive relationship would be expected in this plot. However, there is actually a statistically significant ($P < .05$) negative relationship that explains <1% of the variation.

imum photosynthetic rate were reproduced by the TAD model (Wright et al. 2004). Other realistic relationships include the positive relationship between photosynthetic capacity and xylem sap-flow per leaf area or stomatal conductance (Meinzer 2003), the relationship between the leaf area index (leaf area per ground area) and maximum net photosynthetic rate (Canham et al. 1994), the negative relationship between nitrogen use efficiency and water use efficiency (Field et al. 1983), and the well-established positive relationship between area-based maximum photosynthetic rate and leaf nitrogen per area (Wright et al. 2004). These relationships between dependent traits are not programmed into the TAD model but rather arise as the outcome of interactions among the 34 independent traits that are under selection. The r^2 values for some of these bivariate relationships are relatively low, but this is also the case for field measurements. This realism in relationships among the dependent traits is reassuring.

Beyond the concern that trait relationships in the model results should be realistic qualitatively, it is desirable that the absolute values of traits also be reasonable. We therefore compare the range in values for dependent traits with published data (table A1 in the online edition of the *American Naturalist*). The values for dependent traits are not programmed into the model but arise in the optimal resolution of trade-offs among the independent traits. The values for 16 of 19 dependent traits fall well within their natural ranges; the other three traits are only slightly outside their natural range (table A1). In the case of wood density, and both minimum leaf and minimum xylem wa-

ter potentials, the evolved values were a bit too low and leaf nitrogen content high because moisture conditions in the simulations were higher than normal in most environments. The traits of the diverse seedling designs identified in the simulations are consistent with observations in nature, a conclusion that is further supported in a more detailed presentation of the TAD model (Marks and Lechowicz, forthcoming).

Discussion

Alternative Functional Designs

Our hypothesis of alternative functional designs as a consequence of multiple interacting trade-offs was supported by the TAD simulations. The 100 program runs stabilized on 100 different optima with wide variation in trait values, suggesting that there may in fact be thousands of quantitatively variant optima within this model framework. This abundance of optimal designs implies that different lineages evolving in identical environments are highly unlikely to evolve the same combination of trait values. For example, when comparing only the five designs with the highest fitness among the 100 optimal design types, two-thirds of the 34 independent traits varied by a factor of two or more. This large variation indicates that these optima represent alternative functional designs and are not merely slightly different versions of the same design, a conclusion also supported by the separation of optimal designs in the cluster analysis (figs. 2, 3).

Table 1: Linear regression relationships between dependent leaf trait values for the 37 best designs selected in our test environment

Independent variable	Dependent variable	Adjusted r^2
Leaf blade nitrogen concentration per mass	Maximum net photosynthetic rate per mass	.89
Leaf mass per leaf area	Leaf blade nitrogen concentration per mass	.75
Leaf mass per leaf area	Maximum net photosynthetic rate per mass	.62
Maximum net photosynthetic rate per area	Total xylem sap flow per leaf area	.33
Maximum net photosynthetic rate per area	Seedling leaf area index	.33
Leaf nitrogen use efficiency	Leaf water use efficiency	.31
Maximum net photosynthetic rate per area	Leaf blade nitrogen concentration per area	.29
Maximum net photosynthetic rate per area	Maximum realized stomatal conductance	.19

Note: Relationships included in the table had $P < .01$. The r^2 values for these untransformed relationships are comparable with those observed in field data from natural tree seedlings.

A number of models of plant form and function have found alternative designs, but the alternative designs were generally interpreted as a result of differences in selection regime associated with frequency dependence or environmental differences (Farnsworth and Niklas 1995; Niklas 1997*b*; Schwinning and Ehleringer 2001; Warren and Topping 2001; Mustard et al. 2003). For example, in an elegant model, Niklas (1994, 1997*a*, 1999) showed that trees can have alternative architectures depending on the relative importance of fitness of mechanical stability, seed dispersal, and light interception. In contrast, reviews on adaptation have mentioned the idea that alternative designs might be fit in the same environment for a long time (Bock 1959, 1976, 1980; Lewontin 1978; Gould and Lewontin 1979; Mayr 1983; Gould 1989; Parker and Maynard Smith 1990; Körner 1991; Losos and Miles 1994; Niklas 1997*b*; Gutschick 1999). Most of these reviews discuss alternative designs conceptually and give few if any examples, which can give readers the impression that alternative designs are a rare occurrence in nature—only an interesting exception in a general trend toward convergence to a single optimal design in a given environment. Our results demonstrate that there is such a large potential for alternative designs in the same environment that different lineages almost inevitably will evolve toward different optimal designs. Furthermore, alternative designs dramatically affect most functional traits, suggesting that aside from environmental heterogeneity, alternative designs are a major, if not the main, cause of functional diversity in nature.

Alternative designs also are recognized in a number of models of abiotic complex systems. For example, in applications of GAs to engineering design problems, multiple alternative designs typically are found, including ones that are very similar to successful designs previously developed independently by human designers (Bentley 1999; Koza et al. 1999). Similarly, in the evolution of simple artificial life forms, multiple designs usually evolve (Kauffman 1993; Sims 1999; Yedid and Bell 2002; Chow et al. 2004). What

is unique about our results is that they were obtained with a biologically realistic model of a higher organism in which design outcomes can be directly compared with empirical data (Marks and Lechowicz, forthcoming).

It is likely that there is a general mathematical basis to the emergence of alternative designs in any complex system involving interactions among traits. Consider a very simple model involving only two individual traits (A and B) and a composite trait (C) that is a function of traits A and B . For example, assume $C = A + B$. If keeping trait C at some constant intermediate value maximized fitness (i.e., stabilizing selection on C), then there obviously are multiple alternative combinations for the values of A and B that yield the optimal value for C —any increase in the value of A could be compensated for by a decrease in the value for B . Consequently, there would be an infinite number of optimal combinations for the values of traits A and B . Extending this simple example to more trade-offs among a greater number of traits, it is clear there is no theoretical limit to the number of potential alternative designs that might emerge in a complex system.

A detailed biological example on these same lines recently described in the jaws of labrid fishes provides further illustration of the alternative design concept (Alfaro et al. 2004, 2005). Labrid fish jaws consist of a four-bar mechanism. The shape of the four-bar affects the maximal kinematic transmission coefficient (or max KT) in a redundant fashion, and max KT is significantly correlated with labrid fish ecology. Consequently, there are multiple combinations of jawbones or jaw designs that produce the same ecological performance.

Any complex system of trait interactions comprising a holistic model of organism function contains numerous examples of similar measures of performance that depend on multiple independent traits. For example, in our TAD model, seedling water use depends on root traits for water uptake, xylem traits for water conduction, and stomatal control traits for regulation. Similarly, the nitrogen and

light economy are affected by several traits. The most dramatic example is the carbon economy, which is affected by every structure within the plant because all structures have a construction and maintenance cost. Furthermore, survival and growth and thus plant fitness depend on the interaction among the water, nitrogen, light, and carbon use strategies. Consequently, there is a large potential for alternative functional designs in tree seedlings, and a similarly high potential can be expected in all organisms whose performance depends on the complex interaction among numerous traits.

Approximate Fitness Equivalence of Alternative Designs

Many of the optimal designs found by the GA in our test environment had a similar high fitness (fig. 1); more than one-third of the optimal designs reached a fitness within the top 20% of the range. These alternative designs exploit available resources in different ways but to the same net effect in terms of growth. This provides a potential explanation for the frequent observation of saplings growing equally well at the same site despite large trait differences. In the forestry literature, there are many records of co-occurring tree species capable of similar growth rates despite substantial trait differences (Goulden 1996; Oliver and Larson 1996; Becker et al. 1999; Valladares et al. 2002; Cavender-Bares et al. 2004b). We expect that future research will reveal many examples of equicompetent alternative designs, particularly in the more diverse forests of the tropics.

Although it is not feasible to do laboratory experiments with tree evolution to test the alternative design hypothesis directly, the results of experimental evolution studies with bacteria are remarkably similar to the results of our modeling study with tree seedlings (Travisano et al. 1995; Korona 1996; Nakatsu et al. 1998; Velicer and Lenski 1999; MacLean and Bell 2003). For example, Korona (1996) found that six replicates of a bacterial culture derived from the same clone evolving under identical conditions reached the same fitness level once the cultures stabilized. The fitness increase was proportional to an increase in growth rate, but in each case different trait combinations produced this increase. MacLean and Bell (2003) found that in an adaptive radiation of a bacterium to different growth media, there was no correlation between medium and genetic similarity of the optimal types, implying that the necessary adaptive change was achieved in many different ways. The similarity of results for organisms as different as bacteria and trees suggests that multiple optima of approximately equal growth rate likely also occur in other groups of organisms that display great trait diversity within habitats.

Perspectives

The large potential for the evolution of diverse alternative designs has some interesting ecological implications. In particular, we found that species representing alternative designs might nonetheless differ by only a few percent in fitness (i.e., growth rate). Although such small differences in fitness should promote species coexistence, indefinite coexistence would still require a stabilizing mechanism such as density- or frequency-dependent mortality (Chesson 2000). However, when fitness differences are small, as in the best designs in our results, even weak stabilizing mechanisms are sufficient to insure coexistence (Chesson 2000), and field ecologists have elucidated an abundance of such weak stabilizing mechanisms. In this sense, the existence of alternative designs of approximately equivalent fitness not only supports the evolution of diversity in functional plant traits but in conjunction with weak stabilizing mechanisms also augments species diversity within relatively uniform habitats.

Conclusions

The model results we presented provide an adaptive explanation for the frequent observation of tree seedlings growing equally well at the same site despite large trait differences among species. Such an explanation is timely because the widespread occurrence of large niche overlap is receiving more and more attention in field studies (Ricklefs 2000; Pitman et al. 2001; Valencia et al. 2004) and in theoretical models (Bell 2000; Hubbell 2001, 2005). We suspect that niche overlap is as important in community assembly as are niche differences and that this large overlap in niches is at least in part a consequence of the evolution of alternative functional designs.

According to conventional wisdom, trait diversity evolves only in response to environmental heterogeneity as predicted by the single trade-off optimization models (Levin and Muller-Landau 2000), but our holistic model demonstrates that even in the absence of heterogeneity, separate lineages evolve large trait differences. Therefore, alternative functional designs provide a convincing explanation for the large within-site trait variation observed in forests all over the world.

Acknowledgments

We would like to thank D. Ackerly, G. Bell, J. Cavender-Bares, A. Gonzalez, D. Schluter, D. Tilman, and two anonymous reviewers for commenting on an earlier version of the manuscript. We also thank K. Arai, M. Futer, T. Linkosalo, and R. Roy for their support. We are grateful to the Natural Sciences and Engineering Research Council (NSERC), McGill University, and Groupe de Recherche

en Écologie Forestière Interuniversitaire for generously providing scholarships for C.O.M. The research was funded by an NSERC grant to M.J.L.

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Associate Editor: Mark Westoby
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