

Evolutionary walks through a land plant morphospace

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Abstract

A model for mimicking land plant evolution is here expanded and re-evaluated. The model consists of (1) a morphospace containing on the order of 10^9 phenotypic variants, (2) 15 different fitness landscapes, each defined on the basis of performing one or more of four tasks (i.e. maximizing light interception, mechanical stability and reproduction, and minimizing total surface area), and (3) an algorithm driving a search through fitness landscapes for more fit variants. The model is used to predict the effects of the number of simultaneously performed tasks ('complexity'), abrupt changes in environmental conditions (mimicked by random replacement of one fitness landscape with another), and developmental barriers (mimicked by barring searches from entering specific subdomains in the morphospace) on number and accessibility of variants occupying fitness maxima. The model predicts that (1) the number and accessibility of fitness peaks will increase (while the difference between the relative fitness of peaks and valleys will decrease) in proportion to functional complexity, (2) abrupt shifts in landscapes will increase rather than decrease phenotypic diversity, and (3) obstructed searches have an equal or higher probability of reaching fitness peaks than unfettered searches. These results follow axiomatically from the way hypothetical variants are spatially ordered in the morphospace, the manner in which relative fitness is defined, and the protocol used to locate fitness peaks. A critique of the model's predictions and desiderata for future research are provided.

Key words: Evolution, plants, morphospace, relative fitness, adaptation.

Introduction

Nothing in evolutionary biology has inspired more debate than the pervasiveness of adaptive evolution (Eldredge

and Gould, 1972; Ayala, 1974; Gould and Eldredge, 1977; Stanley, 1979; Lewin, 1980; Templeton, 1980, 1982). The heart of this debate is whether selection pressure is typically strong or comparatively weak. If the former, then the attributes of species are adaptations in the sense that they have been shaped by persistent and strong environmental sorting. If not, then most species are neither more nor less fit than their contemporaries, they simply manage to survive because their differences go largely undetected by natural selection.

This debate is not easily resolved because many of the traditional disciplines of evolutionary biology offer limited insight when taken in isolation. For example, paleontological studies draw attention to the inequality of species preservation and the individualistic nature of species histories (Kidwell and Flessa, 1995; Jablonski and Sepkoski, 1996) such that interpretations of past environmental sorting events are likely biased in favour of potentially idiosyncratic species with easily preserved body parts. Likewise, genetic and ecological studies provide examples of non-adaptive and adaptive evolution, but the spatial and temporal scales they deal with typically preclude synoptic statements about long-term historical processes (Whittaker, 1977; Valentine *et al.*, 1991; Ricklefs and Schluter, 1993; Brown, 1995).

For these and other reasons, some workers have turned to modelling the effects of evolutionary forces not to resolve the prevalence of adaptive evolution so much as to expose how *a priori* assumptions about these forces influence our perception of evolutionary processes. Sewall Wright proposed the best known of these models, one that envisions evolution as a 'walk' over 'fitness landscapes' in search of 'adaptive peaks' (Wright, 1931, 1932; Provine, 1986). The core of this model is a domain containing all of the allelic combinatorial permutations that a hypothetical population can produce. By assigning relative fitness values to the variants in this 'genospace' and animating a search for more fit genotypes with population genetic equations, Wright attempted to show

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how evolutionary forces dictate the prevailing genotypes in populations.

Even though Wright's model is impractical (i.e. the number of allelic combinations that even a small population can theoretically produce is on the order of 10^{800} , while as many as 10^3 axes are required to order variants spatially in even a simple 'genospace'), his model continues to be a useful pedagogic tool, inspiring countless questions about the dynamics of life's history. Indeed, his protocol has been successfully recast in terms of spatial domains containing all (or at least many) conceivable morphological variants ('morphospaces' *sensu* Thomas and Reif, 1993). Perhaps the best known of these models was constructed by David Raup who simulated a morphospace for gastropod, bivalve, brachiopod, and cephalopod shell shape (Raup and Michelson, 1965; Raup, 1966, 1967, 1968; Raup and Stanley, 1971). Raup reasoned that subdomains containing the shapes of many species likely correspond to adaptive peaks, while unoccupied regions likely represent 'maladaptive valleys'. In fact, gastropod, bivalve, brachiopod, and cephalopod shell shapes occupy virtually non-overlapping regions, presumably because they are adapted to particular environmental demands. Equally useful morphospaces have been developed for a variety of different organisms (Gould *et al.*, 1985; Foote, 1990; Ellers, 1993; Thomas and Reif, 1993; Wagner, 1995; Stone, 1996).

In this paper, I review the construction of a morphospace for early land plants (Niklas and Kerchner, 1984; Niklas, 1997*a, b*) and show how it can be used to assess the consequences of abrupt environmental changes and developmental barriers on the number and accessibility of phenotypes occupying local fitness optima. Environmental change is simulated by randomly substituting fitness landscapes as a search for progressively more fit variants proceeds through the plant morphospace. Here, the objective is to evaluate assumptions about the stability of morphology in the face of changing environmental challenges. The effects of developmental barriers are simulated by obstructing searches from entering specific subdomains in the morphospace. The objective of these simulations is to evaluate whether developmental constraints *per se* confine morphological diversification.

Orderings, topologies, and protocols for evolutionary walks

The results of any model purporting to simulate evolutionary dynamics can only be interpreted in the context of the logical (mathematical) confines of the model. Therefore, it is necessary first to discuss these confines, which, for the model at hand, involve three elements: how the morphospace is constructed (ordering), the number and position of fitness maxima and minima

(topology), and the rules governing how an evolutionary walk proceeds to locate more fit variants (search protocol).

Orderings

The spatial arrangement of variants in any morphospace is dictated by the mathematical parameters used to simulate morphology, the numerical values assigned to them, and how both are arranged to render the shape of the morphospace. Only three parameters are required to construct the simplest morphospace for early vascular land plants: the bifurcation angle ϕ , the rotation angle γ , and the probability of branching p (Fig. 1). Assigning uniform ascending numerical values to each of these parameters and aligning the three resulting numerical axes orthogonally produces a Cartesian space. Nevertheless, a far more complex, multi-dimensional space is required because many morphological parameters are otherwise ignored (e.g. stem girth and length) as are the differences that may exist between paired branches resulting from shoot apical divisions. Indeed, the *de minimus* requirement is to assign separate numerical

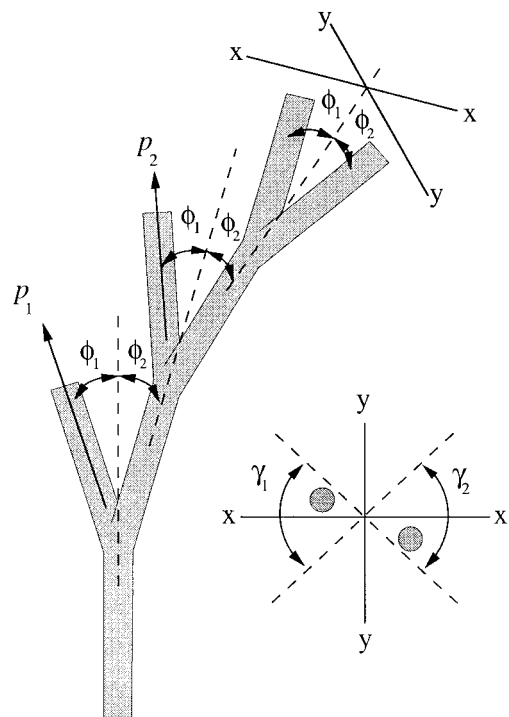


Fig. 1. Parameters used to simulate bifurcate branching structures resembling vascular land plant morphologies. The three parameters are the bifurcation angle ϕ (the angle between the longitudinal axes of each bifurcate pair), the rotation angle γ (the angle between the longitudinal axis of each pair and the horizontal plane), and the probability of apical bifurcation p . Simple isotomously branched structures require equal numerical values for each parameter for each axis in a bifurcate pair (not shown). More complex anisotomously branched structures require separate numerical values for each parameter for each axis (e.g. ϕ_1 and ϕ_2). See text for further details.

values for each of the three parameters to each axis in a pair (Niklas, 1995).

The spatial arrangement of variants in a morphospace is far from trivial because the topology of fitness landscapes and thus the course of a search for more fit variants are dictated by the geometry of a morphospace. The difficulty lies in the fact that a variety of criteria exist for selecting among competing arrangements. Variants could be ordered based on known or inferred developmental relationships among the parts of the organisms in question. Broad morphological trends preserved in the fossil record may be used in conjunction with this approach (Saunders and Work, 1996). Alternatively, the mathematics used to describe the geometry and shape of variants may serve as a rationale for ordering (David *et al.*, 1996). But, in each case, variants are ordered on the basis of the criterion of 'ease of passage' which is based on the *a priori* and thus arguable supposition that organic form ineluctably evolves along more or less continuous morphological transformation series. This may be so, especially when development, history and mathematics point to concordant ordering systems for a particular group of organisms. But all current methods are subjective and thus suspect.

For early terrestrial metaphytes, however, development, history and morphology converge on the same ordering of variants. The fossil record shows that the most ancient tracheophytes branched by the repeated dichotomization of apical meristems, while subsequent species evolved the capacity to produce axillary apical meristems that often branched in the same manner (Stewart and Rothwell, 1993; Taylor and Taylor, 1993). The fossil record also indicates that the most ancient of these plants consisted of sparsely, more or less equally branched and leafless cylindrical axes with small bifurcation angles and non-planated branching patterns. Subsequent evolutionary modifications led to larger more profusely branched plants consisting of unequally branched and over-topped axes many of which had a tree-like appearance (i.e. a main 'trunk' bearing variously configured lateral branching systems). Thus, a reasonable spatial ordering of variants in the morphospace is achieved by assigning decreasing rotation angles and increasing bifurcation angles and probabilities of branching to the axes used to construct the morphospace. When this is done, the most ancient morphologies (e.g. *Cooksonia* and *Steganotheca*) cluster in one corner of the Cartesian space and more derived morphologies (e.g. *Rhynia* and *Psilophyton*) lie along a diagonal transect to the opposing corner of the space which contains the most derived plant morphologies (e.g. *Archaeopteris* and *Lepidodendron*, Fig. 2).

Specifically, all morphological variants in the morphospace consist of three or more untapered, cylindrical axes with uniform terete transverse cross sections. The simplest and presumably most ancient variant in the morphospace

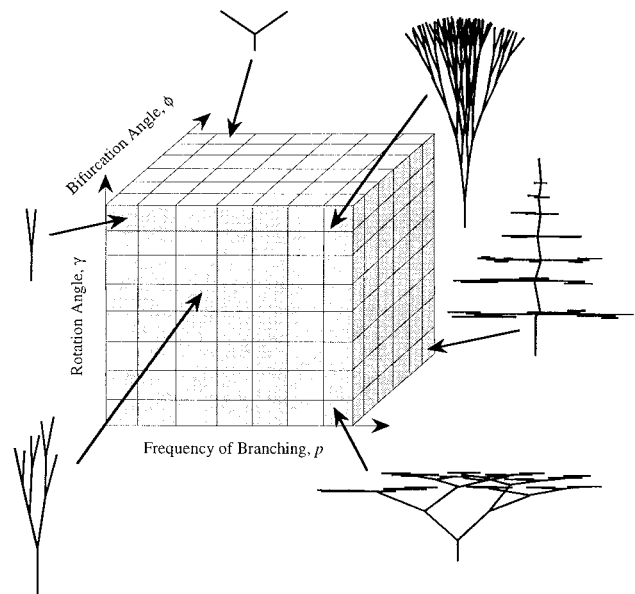


Fig. 2. Simplified three-dimensional morphospace and representative branching structures for vascular land plants based on the orthogonal alignment of three axes representing the numerical values of the bifurcation angle ϕ , the rotation angle γ , and the probability of branching p (see Fig. 1). Y-shaped branching structures reminiscent of *Cooksonia* sporophytes occupy the upper left region of the morphospace; more complex structures with overtopped 'stems' and planated lateral 'branches' occupy the lower right portions of the morphospace (rear and foreground, respectively).

is a Y-shaped morphology reminiscent of early terrestrial metaphytes like (Fig. 2). To simulate more complex morphologies, the simple Y-shaped variant is modified by the addition of more axes. These higher-order branched variants were simulated by permitting a total of 24 bifurcation events (each designated by N). The first formed or most basal axis in all higher order branching variants was arbitrarily designated as nodal level 24 (i.e. $N-0$); all axes generated at nodal level 1 were terminal axes (i.e. $N-23$). Each terminal axis was assumed to bear a 'sporangium' at its free end. Branching patterns with varying degrees of bifurcation were simulated by specifying the probability of bifurcation, p (at each successively lower nodal level of branching) according to the linear formula $p = 23P_{n-(k+1)}/(N+k)$, where $P_{n-(k+1)}$ is the probability of termination at the next nodal level and $N+k$ denotes the previously generated nodal level.

Different values for p , ϕ , and γ were assigned to each of the apices of an initially Y-shaped variant to simulate higher-order branched variants (Fig. 1). The resulting morphospace consisted of two regions or broad subdomains, the simpler of which contained variants whose axes had equal probabilities of branching ($p_1 = p_2$), equal bifurcation angles ($\phi_1 = \phi_2$), and equal rotation angles ($\gamma_1 = \gamma_2$). Within this subdomain, each of the three variables served as an orthogonal axis in a Cartesian space. The second subdomain contained morphological variants

for which $p_1 \cong p_2$, $\phi_1 \cong \phi_2$, and $\gamma_1 \cong \gamma_2$. Thus this subdomain contained variants with a main, more or less vertical axis bearing lateral branching systems with varying sizes, branching angles, and degrees of planation. The resulting morphospace is thus a multi-dimensional domain (currently containing on the order of 10^9 different phenotypic variants) that defies graphic reduction.

Topologies

The relative fitness values of variants in any morphospace can change depending on how fitness is gauged, even though the ordering of variants in the morphospace remains the same. For example, based on the equations used to evaluate the ability of hypothetical phenotypes to intercept sunlight, the most fit phenotypes have planated branching systems in which all bifurcate axes are oriented in a single plane parallel to the earth's surface because this configuration minimizes the exposure of axial surfaces to sunlight and minimizes self-shading (Niklas, 1988, 1992). However, this is the least fit arrangement in terms of mechanical support because horizontally cantilevered branches impose the largest bending moments on subtending branches (Niklas, 1992, 1994a). Consequently, even though the spatial arrangements of phenotypes in the morphospace remain the same, variants with high relative fitness based on the performance of one biological task (light interception) can have radically lower relative fitness based on the performance of another task important to long-term survival (mechanical stability).

Relative fitness values were numerically assigned to each variant by evaluating the ability of each variant to perform one or more of four tasks: maximizing light interception (denoted by L), mechanical stability (M) and reproductive success (R), and minimizing total surface area (S). The procedures for quantifying the performance of each of these tasks has been described in detail elsewhere (Niklas, 1997a, b). Since four biological tasks are involved, a total of 15 fitness landscapes exists: four single-task landscapes (denoted as L, M, R, and S), six double-task landscapes (MR, LM, RL, MS, LS, and RS), four triple-task landscapes (LMR, MRS, MLS, and LRS), and one four-task landscape (LMRS).

Search protocols

Each search for more fit variants started in the morphospace corresponding to the location of a simple Y-shaped morphology similar in general appearance to the sporophytes of *Cooksonia* and *Steganotheca*, which are currently the oldest known presumed tracheophytes (Edwards *et al.*, 1992). A computer algorithm assessed the previously assigned relative fitness values of the variants immediately surrounding this Y-shaped morphology and identified which among these had a higher fitness value than the Y-shaped morphology. The search then

moved on to the location of this more fit variant and repeated the process. A fitness differential of 1% was used as the criterion for a variant being more fit than the one previously identified by a step in the search. If no surrounding variant was found to have a higher fitness value, the algorithm moved the search to the location of an equally fit but morphologically different variant. This protocol continued until variants were located that were surrounded by less fit phenotypes, at which point the search terminated (Fig. 3). Because two or more neighbouring variants may have equivalent higher fitness values, each search was permitted to 'branch' at any step.

It cannot escape attention that the fitness differential (here arbitrarily set at 1%) used to identify which among neighbouring variants are 'more fit' reflects the intensity of selection pressure. A small fitness differential, as used here, mimics intense selection pressure because each step in a search for more fit variants discriminates among small differences in relative fitness. Conversely, a large fitness differential corresponds to a low selection intensity because large differences in relative fitness are required to propel a search over a fitness landscape.

Simulations and their interpretations

The model was used to explore the relationship between the 'complexity' of fitness landscapes and the number of phenotypic optima reached by adaptive walks. Since no consensus exists for the definition of biological complexity, it is here operationally defined as the number of biological tasks each variant has to simultaneously perform to grow, survive, and reproduce. This definition removes the sharp dichotomy said to exist between 'object' and 'process' complexity (i.e. the number of different parts in an organic system versus the number of different interactions among them; McShea, 1996) and also reasserts the context dependency of relative fitness. The relationship between complexity and the number of optima located by searches for more fit variants was determined by plotting the number of phenotypic optima reached by searches against the number of tasks that variants had to perform simultaneously.

The model was also used to simulate the effects of developmental barriers and rapid environmental changes on the course of searches for more fit variants. Developmental barriers were simulated by barring searches from entering specific subdomains in the morphospace. Each of the three parameters used to simulate the phenotypes of early land plants could be used to specify a barrier to a search. For example, searches were restricted to subdomains of the morphospace occupied only by equally branched, non-overtopped, or non-planated morphologies (i.e. $p_1 = p_2$, $\phi_1 = \phi_2$ and $\gamma_1 = \gamma_2$, respectively). Searches were made less restricted by permitting them to explore portions of the morphospace

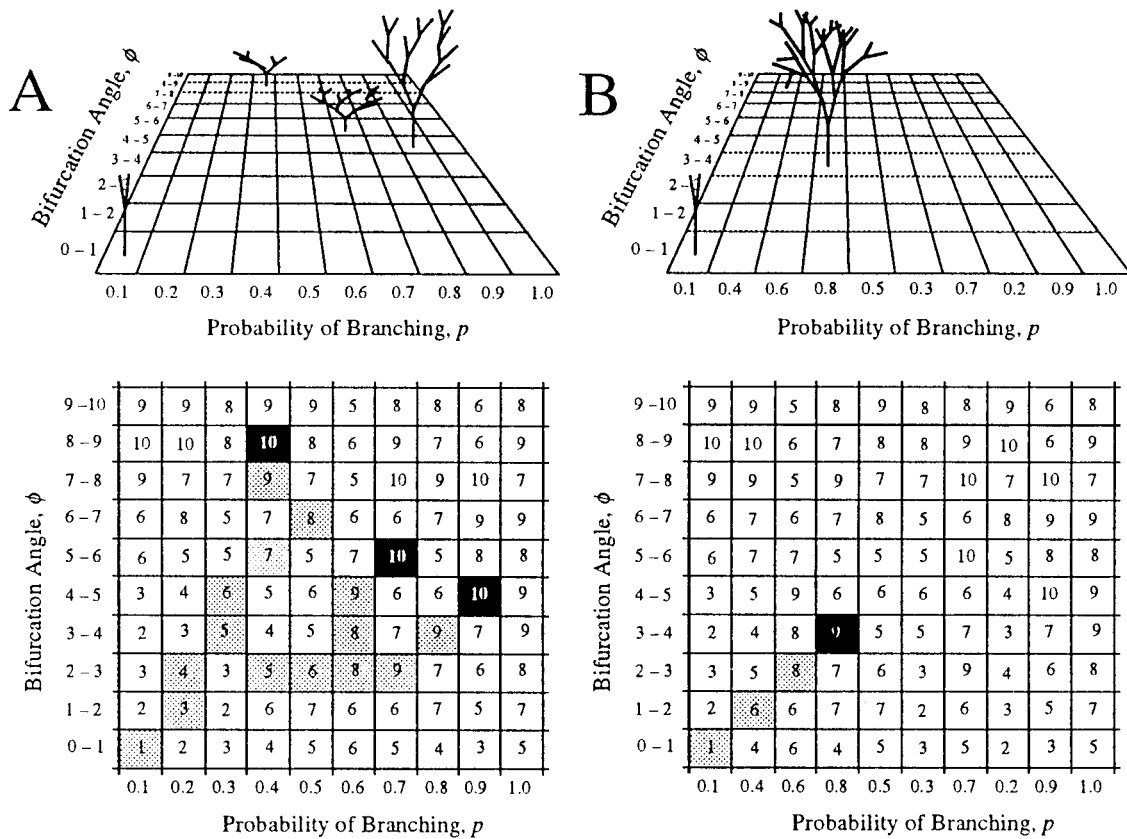


Fig. 3. Effect of re-ordering hypothetical variants over a surface (defined by the bifurcation angle ϕ and the probability of apical branching p) through the morphospace for early land plants (see Fig. 2) on the fitness landscape and the course of searches for more fit variants. In each case, the numerical value of ϕ increases in one degree increments, and the search for more fit variants begins with a branching structure corresponding to $\phi=1^\circ$ and $p=0.1$ (lower left of each surface through the morphospace). The relative fitness values for the variants are indicated by the number in each square (e.g. relative fitness value for the variant with $\phi=1^\circ$ and $p=0.1$ equals 1). Steps in each search are indicated by shaded squares; terminal steps (the locations of accessible phenotypic optima) indicated by black squares. (A) Phenotypic variants ordered by ascending values for ϕ and p . The search for more fit variants has 18 steps, branches twice, and locates three local fitness maxima with equivalent fitness values (i.e. 10). (B) Phenotypic variants ordered by ascending values for ϕ but randomly arranged values for p . The search for more fit variants does not branch and locates one local fitness maximum (i.e. 9). See text for further details.

occupied by equal and non-overtopped branches [denoted by $(p_1=p_2) \cdot (\phi_1=\phi_2)$], or equal and non-planated branches [denoted by $(p_1=p_2) \cdot (\gamma_1=\gamma_2)$], or non-overtopped and non-planated branches [denoted by $(\phi_1=\phi_2) \cdot (\gamma_1=\gamma_2)$].

In terms of simulating environmental changes, a total of 96 landscape substitution sequences exist provided that a search ‘ascended’ from a single-task landscape, into a double-task landscape, then into a triple-landscape, and concluded in the four-task landscape (i.e. $4 \times 6 \times 4 \times 1 = 96$). An additional 72 sequences exist providing an ascending walk ‘descended’ from the four-task landscape into progressively lower-task landscapes and ended in one of the four single-task landscapes (i.e. $1 \times 3 \times 6 \times 4 = 72$). The much larger number of landscape substitutions made possible by randomly selected landscapes was not explored.

Complexity and the number of phenotypic optima

The number of variants that maximized the performance of one task or that optimized the simultaneous perform-

ance of two or more tasks increased in proportion to the number of tasks used to gauge relative fitness (‘complexity’) regardless of whether searches were free to explore the entire morphospace or were barred from exploring specific morphological subdomains (Fig. 4). For example, unobstructed searches through single-task landscapes located, on the average, 2.50 phenotypic maxima, while those through the double-, triple- and four-task landscapes reached, on average, 3.33, 6.25 and 20 phenotypic optima, respectively. On average, the number of phenotypes occupying fitness maxima thus increased in proportion to the number of tasks used to gauge relative fitness. However, the efficiency with which individual tasks were performed decreased in proportion to the number of tasks simultaneously performed (i.e. the fitness differential of landscapes was inversely proportional to the number of tasks used to quantify relative fitness).

The simulations show that the number and accessibility of phenotypic optima increase in direct proportion to biological complexity. This resonates with optimization

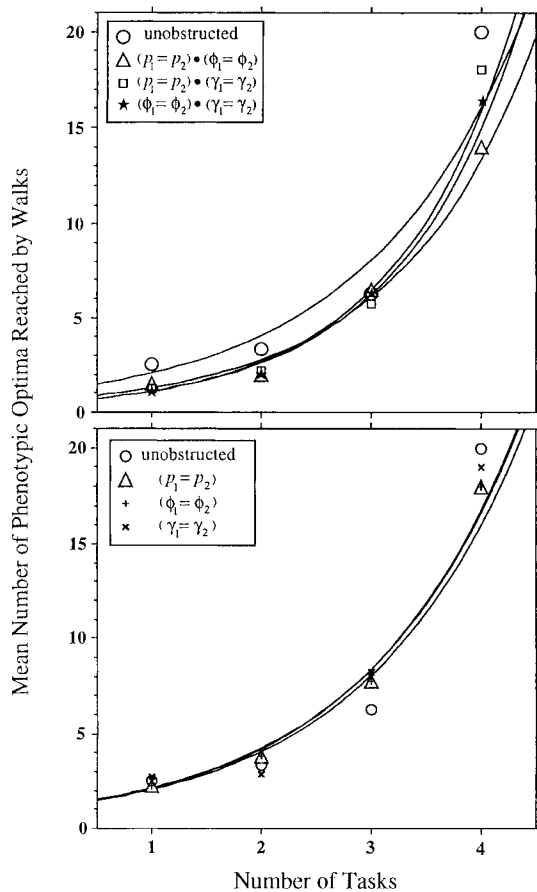


Fig. 4. Mean numbers of phenotypic optima reached by unobstructed and ‘developmentally fettered’ searches for more fit variants plotted against the number of tasks used to gauge the relative fitness values of hypothetical variants in the morphospace for early vascular land plants. In each case, the number of phenotypic optima increases as the number of tasks increases (data taken from Table 1). In some cases, searches barred from entering subdomains of the morphospace (i.e. developmentally fettered searches) reach a greater number of phenotypic optima than those permitted to explore the entire morphospace.

theory which shows that the number of alternative designs for any device increases in proportion to the number of tasks the device simultaneously performs while the efficiency with which each device performs an individual task decreases due to conflicting design requirements (Meredith *et al.*, 1973; Gill *et al.*, 1981; Farnsworth and Niklas, 1995). Arguably, plants are complex ‘devices’ that must harvest solar irradiance, conserve body fluids, sustain self- and dynamic loadings, and disperse spores or propagules. Each of these tasks must be performed concurrently to sustain growth and foster survival and successful reproduction. Some of these biological obligations require morphological or anatomical reconciliations (e.g. light interception and mechanical stability). That the ‘design requirements’ for light interception, mechanical stability and water conservation require some degree of compromise and that the

physical manifestations of equally good compromises are diverse is evident from the ability of morphologically or anatomically dissimilar plant species to survive in similar environments.

Developmental barriers

Searches restricted to exploring the morphospace occupied by equal and non-overtopped branches, or equal and non-planated branches, or non-overtopped and non-planated branches found statistically equivalent numbers of phenotypic optima compared to unfettered walks through the same landscapes (Fig. 4). For example, walks in the triple-task landscape and restricted to the $(p_1=p_2) \cdot (\phi_1=\phi_2)$, $(p_1=p_2) \cdot (\gamma_1=\gamma_2)$ and $(\phi_1=\phi_2) \cdot (\gamma_1=\gamma_2)$ domains of the morphospace located, on average, 6.50, 5.75 and 6.25 phenotypic optima, respectively, while unobstructed walks through the same landscapes located, on average, 6.25 optima. Statistical comparisons among these numbers of phenotypic optima revealed no significant difference at the 1% level. Less restricted searches permitted to explore the morphospace occupied by equally branched, non-overtopped, or non-planated morphologies also found numbers of phenotypic optima equal to those found by unrestricted walks. And, in the case of triple-task landscapes, obstructed searches found, on average, a greater number of optima than that located by unfettered searches through the same fitness landscapes. For example, walks through the single-task landscapes restricted to exploring only the $(p_1=p_2)$, $(\phi_1=\phi_2)$ and $(\gamma_1=\gamma_2)$ subdomains of the morphospace located, on average, 2.25, 2.25 and 2.75 optima, respectively, compared to an average of 2.50 optima located by unobstructed walks; walks through the triple-task landscapes restricted to the $(p_1=p_2)$, $(\phi_1=\phi_2)$ and $(\gamma_1=\gamma_2)$ subdomains located, on average, 8.25, 7.75 and 8.25 optima, respectively, compared an average of 6.25 optima identified by unfettered searches through the same landscapes. Statistical comparisons among these numbers indicated obstructed walks mimicking the presence of ‘developmental barriers’ had either equivalent or a higher probability of locating the same numbers of phenotypic optima compared to ‘developmentally unimpaired’ walks. Nevertheless, comparisons among the relative fitness values of the optima located by obstructed and unobstructed searches revealed that the former had, on average, lower relative fitness values than those of the latter. Thus, although equivalent numbers of optima were located by both kinds of searches, the optima located by obstructed searches were less fit, on average, than those located by unobstructed ‘adaptive walks’.

The ability of barred and unobstructed searches to find, on average, equal numbers of phenotypic optima rests on the ability of searches for more fit variants to branch easily in landscapes, especially in those with low

fitness differentials. Although comparisons between the two show no statistically significant difference, ‘developmentally’ fettered walks in low-task landscapes, which have high fitness differentials and few phenotypic optima, find fewer optima than do unobstructed walks. Also, for some higher-task landscapes, which have low fitness differentials and that contain a comparatively large number of optima (i.e. the triple-task landscape), obstructed walks find more phenotypic optima than unfettered walks. Intuitively, if fitness maxima and minima differ little quantitatively and if many maxima and fitness exist in a landscape, a search barred from proceeding in one direction may have little difficulty in finding an alternative route.

The results of computer simulations for ‘developmentally’ barred adaptive walks agree well with the previously noted influence of functional complexity on the number and accessibility of optima. Since the ‘optima’ located by barred walks have lower relative fitness than those reached by unobstructed walks, logically, there must be an equal or greater number of ‘suboptimal’ phenotypes in landscapes compared to optimal phenotypes and thus there exists a higher probability that barred searches will reach these suboptimal phenotypes as they branch over a fitness landscape.

Environmental changes

Searches ascending from single- to increasingly higher-task fitness landscapes located increasing numbers of phenotypic optima, although, on average, these numbers were significantly less than those reached by searches through stable, unchanging fitness landscapes (Table 1). For example, a mean of 3.33 phenotypic optima were found in unchanging double-task landscapes, while a mean of 2.50 phenotypic optima was located by searches going from single- to double-task landscapes. In contrast, searches descending from the four-task landscapes to lower-task fitness landscapes located, on average, a

greater number of phenotypic optima than either ascending searches or those through stable but otherwise comparable landscapes. For example, searches through the unchanging triple-task landscapes identified, on average, 6.25 phenotypic optima, while those descending into the triple-task landscapes identified, on average, 7.90 phenotypic optima (Table 1).

When the numbers of optima identified by ascending and descending walks are plotted against the number of tasks used to gauge relative fitness, the ascending portion of the graph is concave, the descending portion is convex, and the end-point is higher than the point of origin (Fig. 5). This result indicates that standing morphological diversity will increase as selection pressures focus on the simultaneous performance of more and more biological

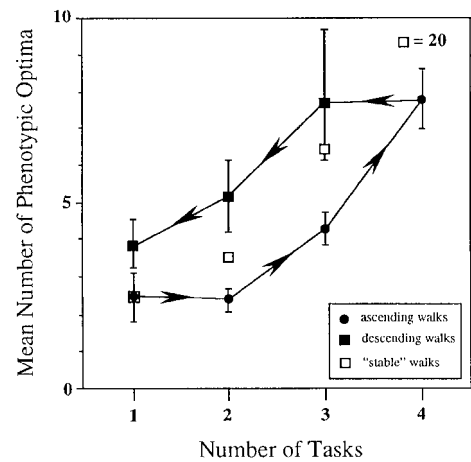


Fig. 5. Means and standard errors of phenotypic optima reached by searches ascending and then descending into lower- and higher-task fitness landscapes plotted against the number of tasks used to gauge relative fitness. The resulting hysteresis-like pattern indicates a larger number of phenotypic optima is found at the end of the cycle than at the beginning. Descending walks also reach higher numbers of phenotypic optima than those reached by searches through unchanging fitness landscapes (‘stable’ walks) defined by the performance of two or three tasks (see Fig. 6).

Table 1. Mean and standard error ($\bar{X} \pm SE$) of the number of phenotypic maxima or optima identified by global searches through unchanging fitness landscapes, and by searches ‘ascending’ and ‘descending’ through fitness landscape substitutions (see Fig. 5)

	$\bar{X} \pm SE$	Number of walks
Searches through unchanging landscapes		
Single-tasks	2.50 ± 0.50	4
Double-tasks	3.33 ± 0.67	6
Triple-tasks	6.25 ± 0.25	4
Four-tasks	20	1
Searches through landscapes ascending from		
Single- to double-tasks	2.50 ± 0.19	24
Double- to triple-tasks	4.18 ± 0.43	96
Triple- to four-tasks	7.91 ± 0.85	96
Searches through landscapes descending from		
Four- to triple-tasks	7.90 ± 1.61	3
Triple- to double-tasks	5.22 ± 1.12	18
Double- to single tasks	3.80 ± 0.87	72

tasks, while standing diversity will decrease as selection pressures focus on a smaller number of tasks but not drop below the original standing diversity initiating the cycle.

That ascending walks find smaller numbers of phenotypic optima than adaptive walks in stable fitness landscapes is undoubtedly a consequence of the relative amounts of time walks are permitted to proceed through these landscapes. Searches for optima through a stable, unchanging fitness landscape are exhaustive in the sense that they have no deadline for their completion, although they are not exhaustive in the sense that they must reach all phenotypic optima. Consequently, each of these searches can complete its exploration of a landscape for variants. In contrast, searches for optima through changing fitness landscapes were arbitrarily truncated whenever a shift from one landscape to another occurs.

However, it is puzzling that descending walks find a higher number of phenotypic optima than exhaustive walks through the same landscapes. No intrinsic property of the model appears to account for this. More phenotypic optima undoubtedly reside in higher-order fitness landscapes than in lower-order landscapes. Assuming that searches have sufficient time to locate optima in higher-order landscapes, every search has a potentially larger number of entry points (previously identified optima) as it descends from a higher-order to a lower-order landscape (Fig. 6). However, there is no reason *a priori* to anticipate that the number of optima found by descending walks should exceed the number found by walks in stable fitness landscapes.

Phenotypic trends

Depending on the sequence of substitution of fitness landscapes, the morphological transformation series identified by searches mimic, with varying degrees of success, the phenotypic transformations purported to characterize the early evolution of vascular land plants (Figs 7–10). In most cases, a respectable number of phenotypic optima bear a morphological resemblance to early Paleozoic terrestrial metaphytes. However, the model provided no ‘unique’ phenotypic series for the evolutionary history of these plants because many equally ‘plausible histories’ can be simulated depending on the sequence of substitution of fitness landscapes.

Two general points are noteworthy, however. First, comparisons among these simulated alternative histories suggest that the necessity to conserve water and minimize total surface area may have played a pivotal role in the early history of land plants, and, second, ascending walks into progressively higher-order landscapes invariably identify increasing numbers of phenotypic optima (i.e. increased ‘diversification’) with more elaborate morphologies than those that came before. All ascending substitu-

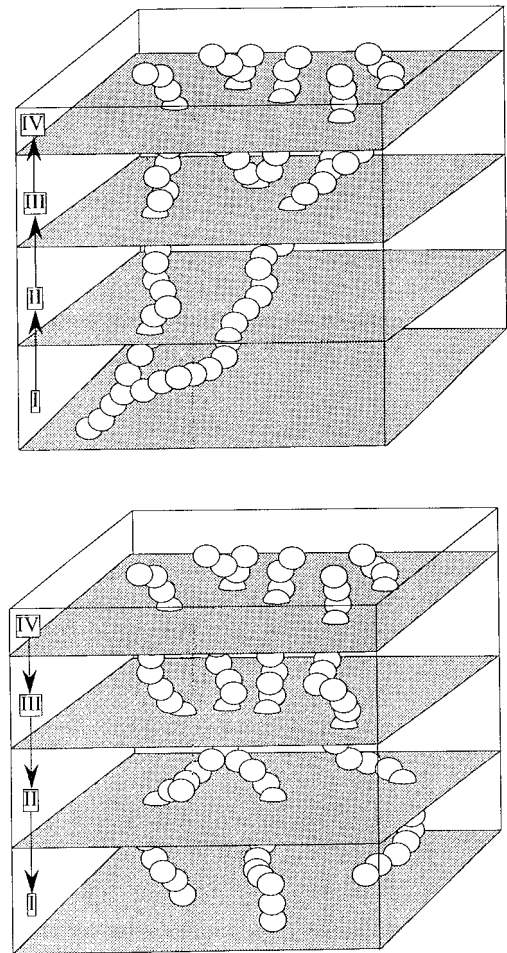


Fig. 6. Diagrammatic rendering of searches for fit variants ascending into higher-task fitness landscapes (top) and then descending into lower-task landscapes (bottom). Fitness landscapes are shown here as shaded flat surfaces; steps in searches for more fit variants are shown as unshaded spheres. Number of tasks used to gauge relative fitness is indicated by roman numerals. Each search entering a lower-task landscape from a higher-task landscape has a greater number of entry points (previously reached phenotypic optima) than each search passing from a lower- to a higher-task landscape. See text for further details.

tion sequences of fitness landscapes beginning with the requirement to minimize plant surface area obtain phenotypic transformation series closely mimicking the broad morphological trends seen in the fossil record for Devonian and Carboniferous vascular land plants (Niklas *et al.*, 1980, 1983; Gensel and Andrews, 1984). Perhaps the most successful of these is the S→RS→MRS→LMRS sequence, which establishes morphologies remarkably reminiscent of ancient rhyniophytes (in the S-landscape), zosterophyllophytes (in the RS-landscape), and trimerophytes (in the MRS-landscape) followed by those similar in appearance to arborescent lycosids and sphenopsides (in the LMRS-landscape) at its closure (Fig. 10). In contrast, all descending walks identify progressively fewer numbers of morphologically less

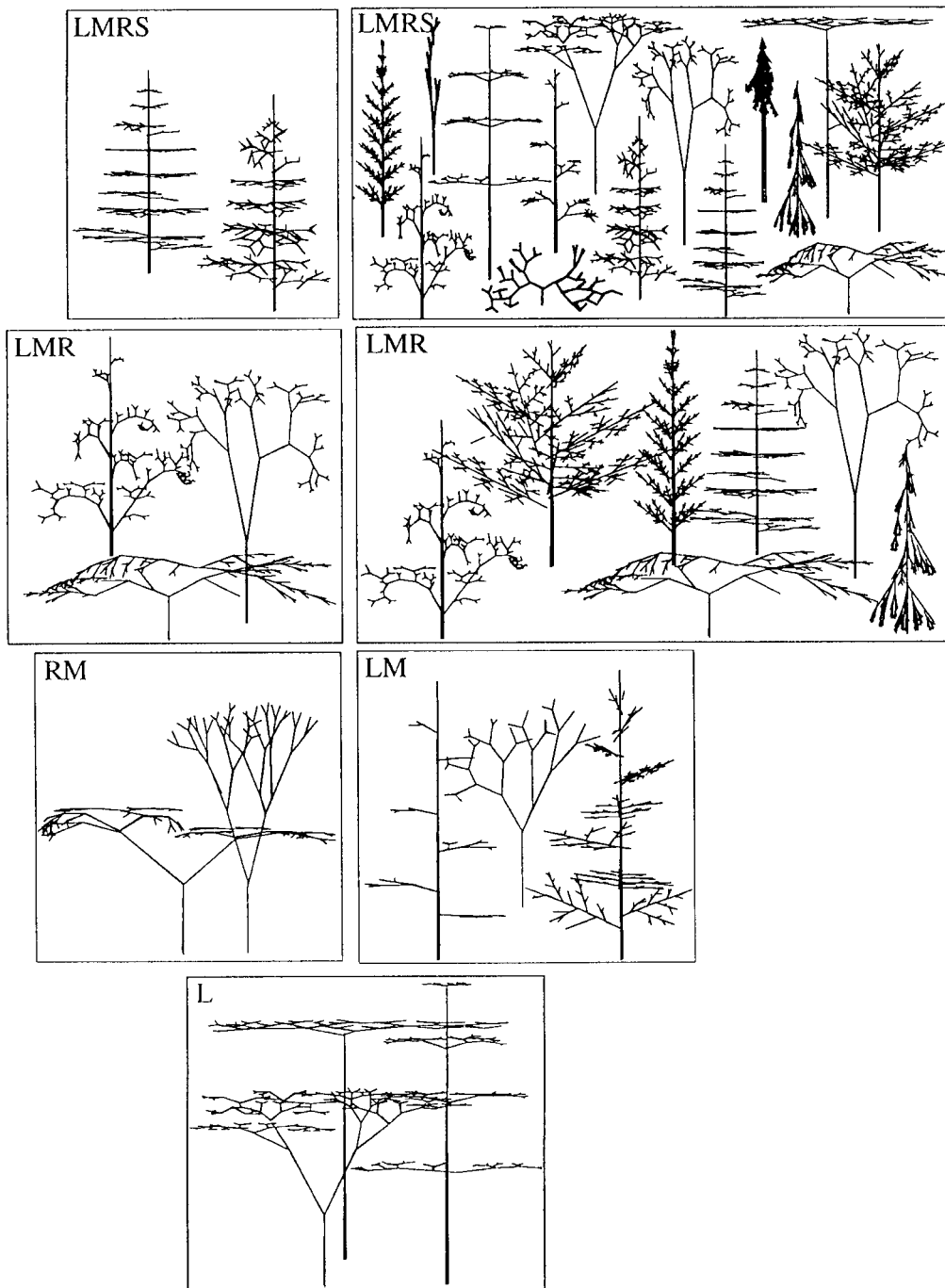


Fig. 7. Appearance of phenotypic optima reached by two searches (left and right) for more fit variants passing from the single-task landscape for the maximization of light interception (bottom) into randomly substituted but increasingly more complex, higher-task landscapes (middle to top). Tasks used to gauge relative fitness in each landscape are indicated by letters: L = maximization of light, M = maximization of mechanical stability, R = reproductive output and potential for long-distance spore dispersal, and S = minimization of surface area.

elaborate forms, which is the opposite of what the fossil record shows to be true.

Truth in advertising

How seriously should this model and its results be taken? The many assumptions required to simulate adaptive land

plant evolution have already been noted, and a significant departure from any of these assumptions must alter the outcome of these simulations. Many of these assumptions can neither be tested experimentally with living plants nor asserted invariably to hold true for extinct ones. Nor can the claim be tested that the history of terrestrial plants was largely an adaptive episode, even though the

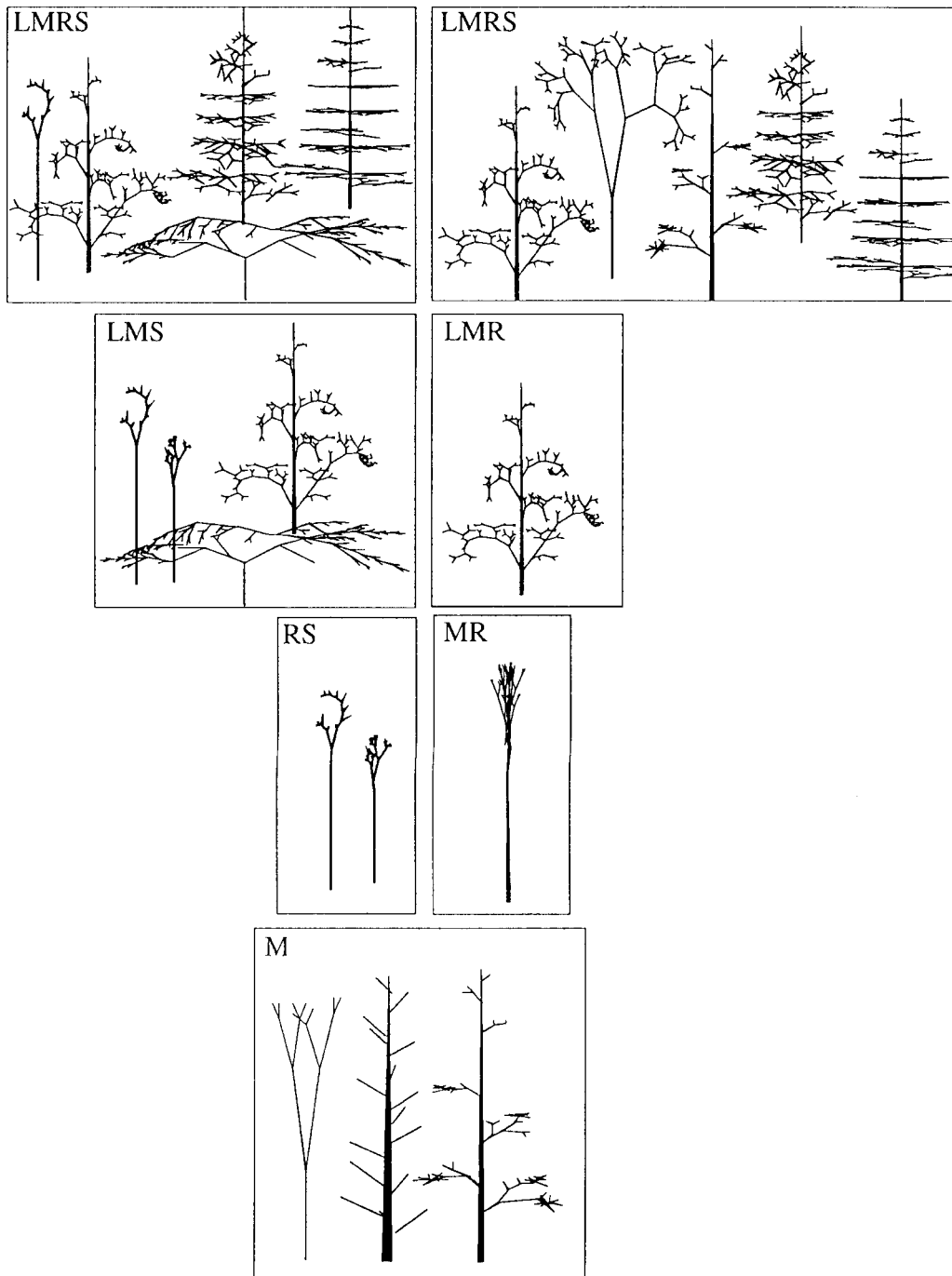


Fig. 8. Appearance of phenotypic optima reached by two searches (left and right) for more fit variants passing from the single-task landscape for the maximization of mechanical stability (bottom) into randomly substituted but increasingly more complex, higher-task landscapes (middle to top). Tasks used to gauge relative fitness in each landscape are indicated by letters (see Fig. 7 legend for notation).

correspondence between simulated and observed early land plant evolution is intriguing. Many models mimic the behaviour of natural systems, but for incomplete or incorrect reasons (Niklas, 1994b).

The model's only current use is to expose how specific assumptions about evolution logically operate *within the mathematical restrictions of the model*. If the simulations

resulting from these assumptions challenge our preconceptions about how the evolutionary process actually works, then a re-examination of these assumptions is warranted. When used in this way, the model's behaviour is instructive. For example, although the magnitude of selection was maintained at a uniform level in all simulations, the numerical difference between fitness maxima

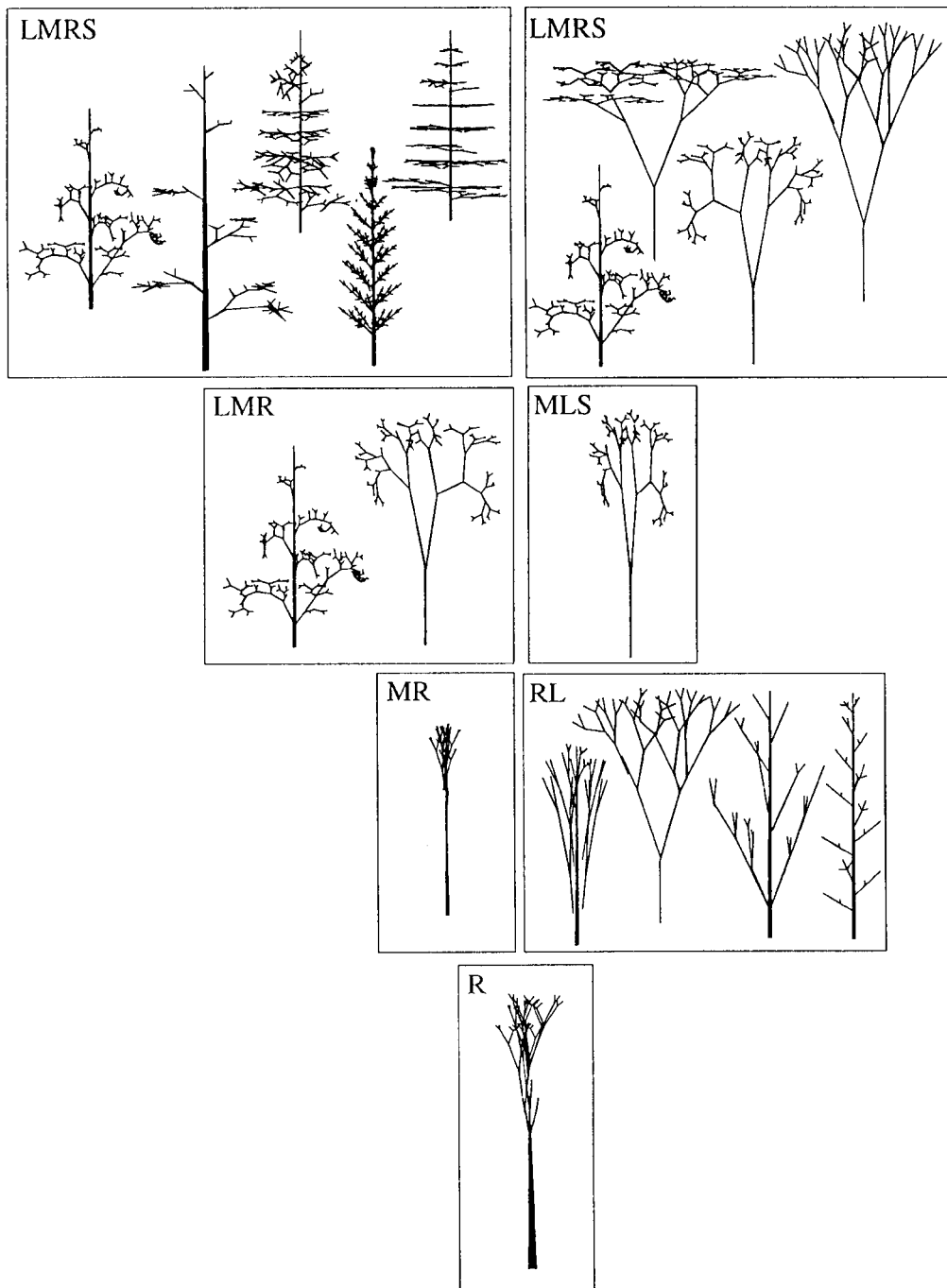


Fig. 9. Appearance of phenotypic optima reached by two searches (left and right) for more fit variants passing from the single-task landscape for the maximization of reproductive output and potential for long-distance dispersal (bottom) into randomly substituted but increasingly more complex, higher-task landscapes (middle to top). Tasks used to gauge relative fitness in each landscape are indicated by letters (see Fig. 7 legend for notation).

and minima is, on average, inversely proportional to the number of tasks whose simultaneous performance influenced relative fitness, whereas the number of phenotypes best equipped to perform these tasks increases. These relationships suggest that morphological diversification is fostered when selection acts on the performance of mani-

fold rather than a few biological tasks influencing growth, survival or reproduction. Since the probability of morphological diversification increases as the focus of selection includes more and more biological functions, there is no reason *a priori* to assume that the morphological horizons available to evolving lineages diminish in response to

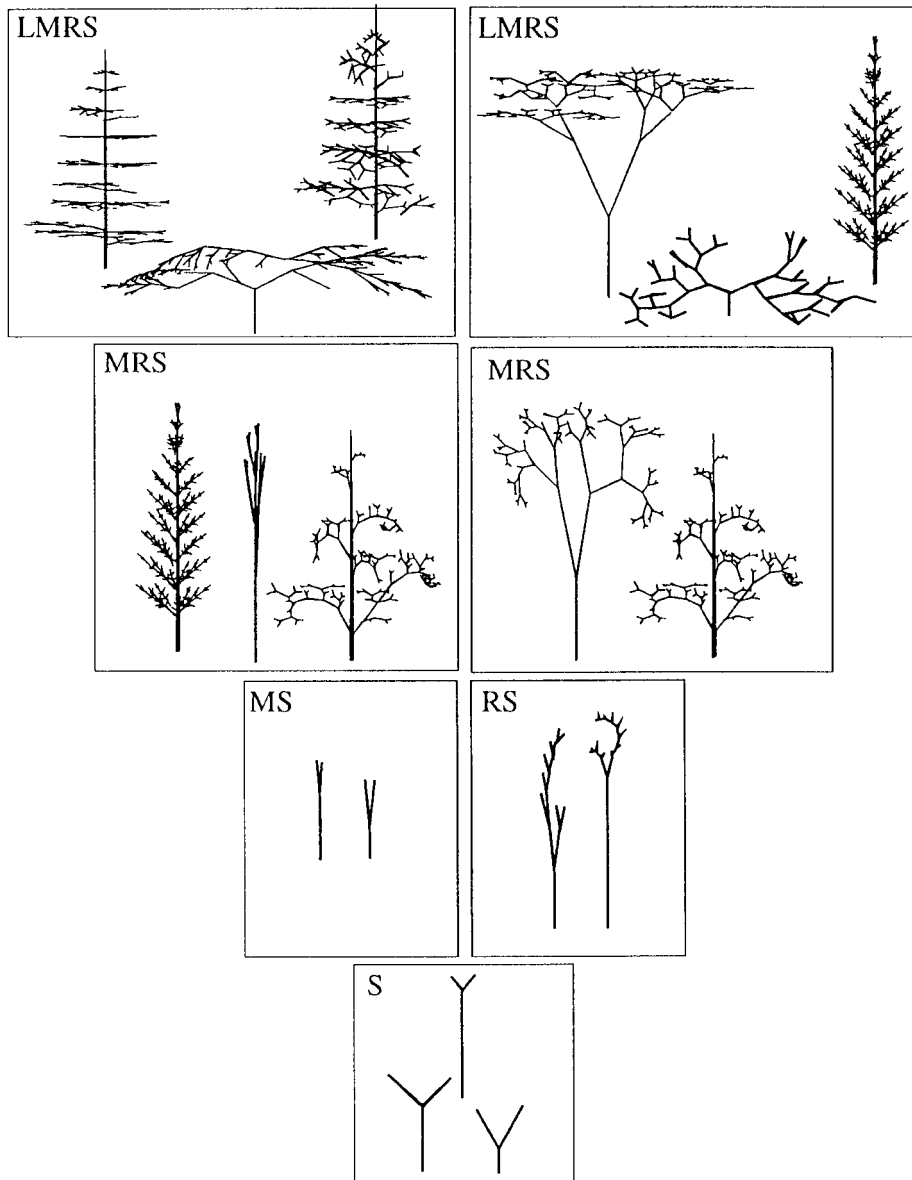


Fig. 10. Appearance of phenotypic optima reached by two searches (left and right) for more fit variants passing from the single-task landscape for the minimization of surface area (bottom) into randomly substituted but increasingly more complex, higher-task landscapes (middle to top). Tasks used to gauge relative fitness in each landscape are indicated by letters (see Fig. 7 legend for notation).

increasing biological complexity regardless of the intensity of selection.

Simulations also indicate that *intense* environmental sorting is required to achieve *adaptive* morphological trends on functionally complex fitness landscapes simply because extremely small fitness differentials exist among variants on these landscapes. In contrast, modest to low intensities of selection appear sufficient to propel a search for more fit variants on functionally simple, single-task fitness landscapes, which have exceptionally high global fitness differentials and comparatively few ‘adaptive peaks’. These features of the model bear on the probability of anagenesis versus cladogenesis and on the likelihood

that evolutionary ‘trends’ are a consequence of diffusive evolution. According to the model presented here, fitness landscapes with low fitness differentials are conducive to cladogenesis and diffusive evolution when selection pressures are modest to low simply because these complex landscapes have smooth topologies with manifold local fitness maxima. A lineage evolving over this kind of landscape can theoretically meander aimlessly, emancipated from the effects of selection to explore much of the morphospace. Since a lineage can morphologically diverge with impunity, the probability of cladogenesis is high. In contrast, evolving lineages will be canalized toward one or a few fitness maxima on simple landscapes with rugged

topologies and thus manifest anagenesis even when selection pressures are comparatively low.

The model further suggests that an adaptive walk for more fit variants is just as likely to locate the same number of fitness optima when barred from specific kinds of morphological transformations as when it is free to venture into any region of a morphospace. The phenotypic optima reached by 'developmentally' fettered walks have, on average, lower relative fitness values than those reached by walks free to explore the entire morphospace over functionally simple fitness landscapes. In contrast, little difference exists, on average, between the relative fitness values of phenotypes reached by fettered and unfettered walks on functionally complex landscapes. This feature of the model is a direct consequence of the low fitness differentials among variants when fitness is gauged on the basis of performing manifold biological tasks. Although there is no legitimate basis for assuming that this phenomenology holds true for real evolving systems, the restrictions of the model caution that there is no reason *a priori* to assume that 'developmental barriers' necessarily restrain a lineage from evolving morphologies that can survive and flourish, especially when relative fitness is correlated with the simultaneous performance of many tasks.

The third prediction of the model is that cycles of expanding and contracting selection pressures obtain a net accumulation of phenotypic variants with high relative fitness despite the extensive elimination of the previously most 'adapted' phenotypes. A search for more fit variants descending through randomly substituted, progressively less complex fitness landscapes finds fewer phenotypic optima compared to the number reached by the search ascending through sequentially more complex landscapes. Nevertheless, the number of phenotypic optima is larger at the end of the search and each of the optima identified at the end of the search can serve as the point of origin for future 'adaptive walks,' environmental perturbations of the sort modelled here theoretically increase rather than decrease standing diversity. It is not possible to identify precisely the reason(s) why the model behaves this way. Intuitively, the phenotypic variants identified by a search descending from more to less complex fitness landscapes are 'generalists' in the sense that they perform manifold tasks well yet no particular task exceptionally well. Although their spatial location in the morphospace is invariant, these 'generalist' morphologies may have a higher probability of being located near local fitness maxima in other landscapes in which fitness is more narrowly defined (i.e. those favouring 'specialists').

Models for organic evolution are still in their infancy and their phenomenologies are thus highly suspect. As formal mathematical models mature and as they are subjected to and withstand the assault of experimental tests using living organisms, evolutionary biologists may

come to rely on these models with more confidence. Presently, however, models for evolution such as that discussed in this paper must be viewed sceptically. At best, they can be currently used as numerical metaphors for exploring assumptions about the complexity of evolutionary processes and mechanisms. This will change only if methods are found to test rigorously models that purport to simulate evolutionary processes accurately. This presents a great challenge. If all the results of a model fail to resonate with historical events, the model must be rejected as wrong or incomplete. But if a model predicts a unique historical pattern that agrees in all its particulars with the evolutionary history of the organisms being modelled, it may do so for all the wrong reasons.

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