

Predicting distributions of species richness and species size in regional floras: Applying the species pool hypothesis to the habitat templet model

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Abstract

The species pool hypothesis is applied here to the interpretation of 'hump-shaped' (unimodal) species richness patterns along gradients of both habitat fertility and disturbance level (the habitat templet). A 'left-wall' effect analogous to that proposed for the evolution of organismal complexity predicts a right-skewed unimodal distribution of historical habitat commonness on both gradients. According to the species pool hypothesis, therefore, the distribution of opportunity for net species accumulation (speciation minus extinction) should also have a corresponding unimodal central tendency on both habitat gradients. Two assumptions of this hypothesis are illustrated with particular reference to highly fertile, relatively undisturbed habitats: (i) such habitats have been relatively uncommon in space and time, thus providing relatively little historical opportunity for the origination of species with the traits necessary for effective competitive ability under these habitat conditions; and (ii) species that have evolved adaptation to these habitats are relatively large, thus imposing fundamental 'packing' limitations on the number of species that can 'fit' within such habitats. Based on these assumptions, the species pool hypothesis defines two associated predictions that are both supported by available data: (a) resident species richness will be relatively low in highly fertile, relatively undisturbed contemporary habitats; and (b) species sizes within regional floras should display as a right-skewed unimodal (log-normal) distribution. The latter is supported here by an analysis of data for 2,715 species in the vascular flora of northeastern North America.

Key words: disturbance, diversity, habitat fertility, 'left-wall' effect, productivity, plant size

Introduction

A number of theoretical models have been designed for predicting patterns in the attributes of terrestrial vegetation across habitat gradients and for interpreting the causes of these patterns on local and regional scales. Most of these models recognize two major envi-

ronmental gradients representing two general, largely independent sources of environmental variation affecting growth and fitness in higher plants: (i) variation in the level of habitat impoverishment or nutrient 'stress', representing the maximum potential fertility of the substrate, or the total nutrient content of the ecosystem; and (ii) variation in the level of disturbance from

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physical forces or consumers causing physical strain, tissue damage, tissue loss, or plant death (Grime 1979; Huston 1979, 1994; Tilman 1988; Taylor et al. 1990). These habitat attributes represent, respectively, variation in the potential 'resource-supplying power' of the habitat and variation in the extent to which this potential can be realized in the accumulated biomass of the resident vegetation, i.e. the proximity to environmental carrying capacity (Taylor et al. 1990). Community biomass or productivity, therefore, is the common currency for measuring the magnitude of each of these habitat attributes; the biomass of vegetation within a climatic region generally increases when there is increasing habitat fertility and when there is decreasing disturbance, with maximum potential, or carrying capacity (for a given level of habitat fertility) realized in the absence of disturbance.

One of the most researched patterns of variation along both of these habitat gradients concerns the wide variation in plant species richness. The pivotal question for this body of research centers on the causes of this variation. Is species richness variation determined by variation in these two major habitat attributes? Is it determined by variation in the currency (i.e. community biomass) by which they are measured? In the proximate sense, of course, the answer to these questions is 'yes' because terrestrial plant life is not supported at all on extremely impoverished substrates or under extremely severe disturbance, where species richness is zero because productivity is zero. Moving along these gradients, as productivity begins to increase, species richness likewise has nowhere to go but up. What is most intriguing, however, is that after reaching a maximum level, species richness usually declines to lower levels again as habitat fertility continues to increase or as disturbance level continues to decrease. The resulting unimodal 'hump-shaped' relationship (Grime 1973, 1979; Connell 1978; Huston 1979) for regional floras has been widely reported and its interpretation has been the subject of numerous empirical and theoretical investigations (Waide et al. 1999; Mittelbach et al. 2001; VanderMeulen et al. 2001).

The interpretation of the monotonic decreasing phase for species richness toward the highly fertile and undisturbed ends of habitat fertility and disturbance gradients remains at the center of controversy (see reviews Rosenzweig & Abramsky 1993; Abrams 1995; Grace 1999; Aarssen 2001). Much of the theory proposed to explain this decreasing species richness pattern involves interspecific competition as the principal underlying mechanism; i.e. relatively low species richness in highly fertile, undisturbed habitats is considered to be a consequence of the relatively high productivity of these habitats, which in turn, is considered to

cause relatively intense competition leading to competitive exclusion (Grime 1979; Huston 1979, 1994; Grace 1999, 2001). Empirical evidence (e.g. see Bonser & Reader 1995; Gaudet & Keddy 1995; Twolan-Strutt & Keddy 1996; Keddy et al. 1997, 2000 and references cited there) indicates that this effect can and indeed does account for why there are generally more species excluded from highly fertile, undisturbed habitats, compared with less fertile or more disturbed habitats. It does not, however, explain why there are relatively *few* species that are *not* excluded from these habitats. This mechanism involving competitive exclusion is, again, only a proximate ecological one, i.e. differences in the measured competitive abilities of species (and hence, the likelihood of competitive exclusion) generally increase under conditions of increasing substrate fertility, or under conditions of decreasing disturbance. In the case of increasing habitat fertility, this may involve switching from nutrient competition to light competition where differences in plant size may lead to higher competitive asymmetry. Decreasing disturbance also increases the intensity of competition by allowing density or biomass to approach equilibrium or carrying capacity, thus allowing differences in competitive ability to exert a stronger effect. Hence, this mechanism only identifies which of the adaptations (i.e. effective competitive ability, especially for light) required for success in highly fertile, undisturbed habitats are lacking in many species and thus explains why these species do not reside there; it does not explain why the adapted (i.e. resident) species in highly fertile, undisturbed habitats are relatively few in number. Accordingly, it does not account ultimately for the decreasing pattern of resident species richness toward the highly fertile, undisturbed ends of habitat gradients (Aarssen 2001).

It is in this latter regard that three additional hypotheses differ from the models of Grime, Huston and Grace referenced above. According to these other hypotheses, the resident species in highly fertile, undisturbed habitats are relatively few in number because: (i) these habitat types have relatively few opportunities for niche differentiation and hence, species compete more intensely here (resulting in competitive exclusion) because of greater niche overlap (*environmental heterogeneity hypothesis*) (Newman 1973; Tilman 1988); or (ii) these habitat types have relatively few opportunities for facilitation between species which, therefore, limits the number of species that coexist (*facilitation hypothesis*) (DiTommaso & Aarssen 1991; Brooker & Callaghan 1998); or (iii) these habitat types have been relatively uncommon and, thus, have had relatively little historical opportunity, in space and/or time, for the origination of species that are adapted with the traits required for effective competi-

tive ability under the environmental conditions of these habitats (*species pool hypothesis*) (Taylor et al. 1990; Aarssen 2001; Schamp et al. 2002).

The role of species pools has received considerable attention in recent empirical studies (e.g. Partel et al. 1996, 2000; Wisheu & Keddy 1996; Zobel 1997; Partel & Zobel 1999; Liira & Zobel 2000; Grace 2001). Theoretical arguments based on historical evolutionary opportunity have also been considered in several discussions and reviews (Hodgson 1987; Rosenzweig & Abramsky 1993; Abrams 1995; VanderMeulen et al. 2000). In the present paper, the species pool hypothesis, as envisaged by Taylor et al. (1990), is taken to greater maturity by applying it explicitly to the habitat templet model (Southwood 1977; Greenslade 1983), depicting habitat fertility and disturbance gradients as independent axes of variation for classifying habitat types and associated plant strategies in the vegetation that they support (Taylor et al. 1990). Using a simple prediction for historical habitat commonness variation and associated opportunities for species accumulation over evolutionary time, together with a simple prediction for species size variation and species size/number 'packing' limitations on the habitat templet, we show that species richness variation can be predicted inevitably as a two-way right-skewed (log normal) unimodal distribution on the habitat templet. The model developed here also predicts a parallel log normal distribution of species sizes across regional floras, which is tested below using data from the vascular flora of northeastern North America.

Predicting variation in historical habitat commonness and opportunity for net species accumulation (speciation minus extinction) on the habitat templet

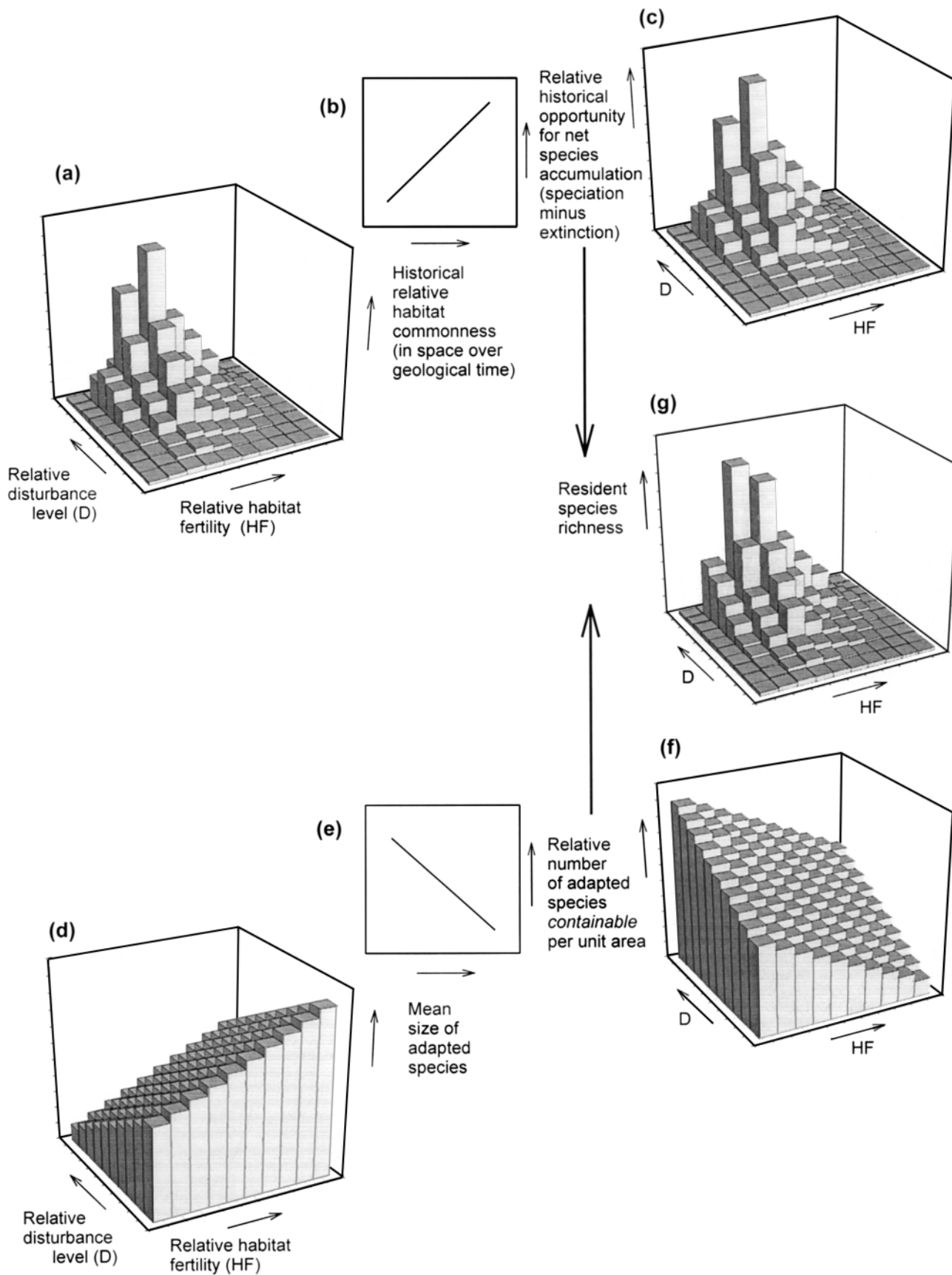
The very first terrestrial habitats must have had extremely impoverished substrates approaching the lower boundary of fertility capable of supporting vegetation. Over evolutionary time, the frequency of habitats with higher fertility must have increased gradually due to the accumulating effects of soil mineralization, nitrification and nitrogen fixation. Other forces would act to reduce habitat fertility, including volcanism, erosion, flooding, leaching and de-mineralization. With these opposing forces acting to simultaneously increase and decrease habitat fertility over time, and with only a lower boundary to fertility, we can postulate a 'left wall' effect similar to that proposed for the evolution of organismal complexity (Gould 1988). Because habitat fertility can increase with no clearly definable upper bound but can decrease only to zero, a

right-skewed unimodal distribution of contemporary habitat fertility can be predicted. Hence, this model assumes that highly fertile habitats are relatively rare because they have generally the youngest geological age. The least fertile habitats, however, although among the oldest in geological age, are not the most common contemporary habitat type because sufficient time has elapsed for most habitat substrates to evolve a more intermediate level of fertility, i.e. because of the 'left wall' effect, the mode increases slowly over time.

Temporary, local patches of relatively high soil fertility would have always been common in most vegetation types because of patchiness in local quantities of decomposing biomass and defecation from animals. Whole habitats with very high fertility (i.e. high total ecosystem nutrient content), however, should be relatively uncommon both in the sense of being relatively young (i.e. with a short geological history) and hence, also in the sense of being relatively diminutive in spatial extent on a global scale, both presently and historically. Historical habitat commonness distribution on a habitat fertility gradient should, therefore, be right-skewed with a relatively long and low right tail (Fig. 1a). Supporting evidence for right-skewed unimodal frequency distributions for contemporary habitat productivity types is available from several recent studies (Brown & Schroeder 1999; Hansen et al. 2000; Schamp et al. 2002).

In addition to extremely impoverished substrates, the very first terrestrial habitats for vegetation would have had no major disturbances from fires, activities of large herbivores (e.g. consumption, trampling) or activities of humans (e.g. cultivation, logging). Over evolutionary time, the level of disturbance can be expected to have increased but, unlike the case for habitat fertility, there would have been no simultaneous opposing forces acting to decrease the level of disturbance. Hence, this model assumes that the increase in habitat disturbance level over time was more rapid and more extensive than the increase in habitat fertility, owing especially to widespread and persistent disturbances from human activities. If we assume, therefore, that habitats with very high disturbance have greater historical commonness than habitats with very low disturbance, then the distribution of historical habitat commonness (in space over time) may also be right-skewed unimodal on a *decreasing* disturbance gradient (Fig. 1a), but would in any event have at least some kind of unimodal central tendency.

Because speciation requires space and time, we may assume that the relative number of species that have originated with adaptation to a particular habitat type must be some increasing function of the historical relative commonness of the habitat type in space and time (Fig. 1b). Similarly, the frequency of extinction might



also be expected to decrease with increasing spatial commonness of the habitat type. Accordingly, the species pool size, defined by the opportunity for net species accumulation (speciation minus extinction) should also have a corresponding right-skewed distribution on both habitat gradients (Fig. 1c). Supporting evidence for a right-skewed unimodal species pool distribution on habitat fertility gradients is evident from an analysis of Ellenberg's indicator values for over 1,700 species of British plants (Fig. 2). The group of plants with the highest indicator value (9), representing adaptation to the most fertile habitats (based on soil nitrogen), has the fewest species followed by the group with the lowest indicator value (1) representing adaptation to the least fertile habitats.

It is important to note that many (perhaps most) plant species have partial adaptation to highly fertile, undisturbed habitats in the sense that they can grow there successfully *if resident species are artificially removed*. In one sense this might suggest that the 'potential' species pool for highly fertile, undisturbed habitats is actually quite large. This may be important in terms of identifying predictions for vegetation change in the event that contemporary resident species become extinct from these habitat types. However, this definition is of limited use for explaining how contemporary patterns of resident species richness came about in natural vegetation. It is with this objective in mind that the species pool hypothesis (as envisaged here and by Taylor et al. 1990) defines the species pool in terms of the pool of available species that are *capable of ongoing successful recruitment within a habitat type in the presence of all naturally resident species*. Hence, the relevant species pool for highly fertile, undisturbed habitats consists of those species that can complete their life cycle and recruit offspring under the prevailing selection pressures, including competition, associated with these habitat conditions (Aarssen 2001; Schamp et al. 2002). Defined in this way, the species pool size for highly fertile, undisturbed habitats is relatively small (e.g. Fig. 2), we suggest, primarily because of the variation on the habitat templet represented in Fig. 1c.

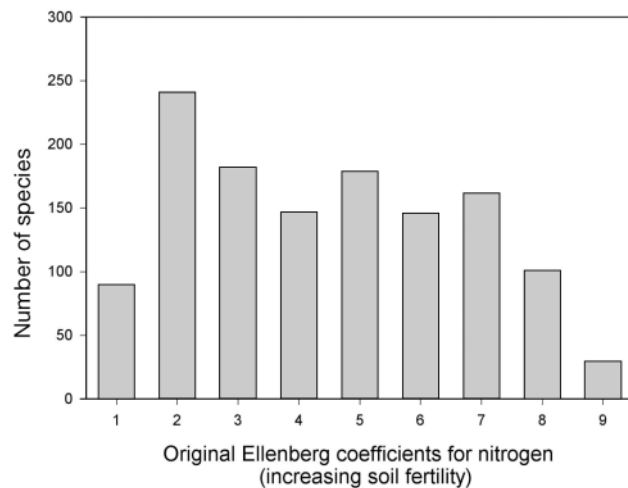


Fig. 2. Frequency distribution of Ellenberg's indicator values for soil nitrogen (a general indicator of soil fertility) assigned to 1,791 species of British plants. Data are from Hill et al. (1999).

Predicting variation in species size and size/number 'packing' limitations on the habitat templet

Fundamental constraints are also associated with species size distributions on the habitat templet. In the most impoverished and/or most disturbed habitats that support vegetation (e.g. deserts, sand dunes, gravel road verges), very large plant size obviously cannot be sustained (e.g. Olofsson 2001). Accordingly, the mean sizes of species that have evolved adaptation to these habitats is necessarily relatively small. In contrast, the evolution of the largest plant sizes has been possible only in habitat types where there is enough time for biomass to accumulate without the limitation of biomass loss resulting from major disturbances, combined with sufficient resource supplying power to support the accumulation of a large biomass (e.g. forests on deep, mesic, fertile soils). Moreover, such habitats favour resident species with relatively tall stature, a product of natural selection associated with

Fig. 1. Assumptions and predictions for variation in historical habitat commonness (a), historical opportunity for net species accumulation (speciation minus extinction) (b, c), mean size of adapted species (d) and the relative number of adapted species 'containable' per unit area (e, f) on the habitat templet. Variation in contemporary resident species richness on the habitat templet (g) is predicted as a product of the combined effect of variation in species pool size (c) and variation in the number of adapted species 'containable' per unit area (f; cf. main text). Note that the disturbance axis increases from right to left in order that the predicted right skewed pattern (with the 'hump' closer to the left, *high* disturbance end of the axis) corresponds with the predicted right-skewed pattern on the habitat fertility axis (with the 'hump' closer to the left, *low* fertility end) (e.g. see Fig. 3). This not only allows more effective illustration in the three-dimensional view but also allows correspondence between the axes at the left end in terms of where biomass is truncated at zero values; i.e. biomass is zero under very *high* disturbance (not low disturbance) just as biomass is zero under very low fertility (not high fertility).

the ‘race to the canopy’ required for minimizing the probability of being overtopped by crowded neighbours engaged in competition for light. Hence, we can expect the mean size of resident plant species within habitats to be some increasing (not necessarily linear) function of both increasing habitat fertility and decreasing disturbance (Fig. 1d). Given the conventional packing rule applied to biotas, where the number and size of objects ‘packed’ (e.g. individuals, species) must inevitably trade-off directly (Fig. 1e) (Brown 1995), the relative number of species that are ‘containable’ per unit area within a habitat should, therefore, be some *decreasing* (not necessarily linear) function of both increasing habitat fertility and decreasing disturbance (Fig. 1f). Because of this species size/number trade-off, the detection of species richness patterns along habitat gradients may be dependent on sample plot size (Oksanen 1996). Hence, whereas a single 100 m × 100 m plot of tropical rainforest may contain hundreds of relatively large plant species, it could be argued that it might contain thousands if they were all smaller in size (e.g. as in the case of insects).

Predicting variation in contemporary resident species richness on the habitat templet

Based on the above theoretical considerations, we may predict that the relative number of resident species in a given habitat type on the habitat templet will be determined, primarily, as a product of two variables: (i) the opportunity for origination (minus extinction) of species with adaptation to the habitat type, i.e. the species pool size (Fig. 1c), which is a function, primarily, of the historical commonness of the habitat type (Figs. 1a, b); and (ii) the number of species that can physically ‘fit’ (per unit area) within the habitat (Fig. 1f), which is a function of the sizes of the species that have evolved adaptation to the habitat type (Figs. 1d, e). The combined effect of these two variables, both of which have right-skewed frequency distributions, produces an even more strongly right-skewed two-way (bivariate) unimodal distribution predicted for contemporary resident species richness on gradients of habitat fertility and disturbance (Fig. 1g). This is consistent with the common ‘hump-shaped’ species richness patterns reported for both gradients from empirical data.

Resident species richness within a given habitat will, of course, also be affected by other factors, including the level of environmental heterogeneity and opportunities for facilitation between species, as well as other historical attributes of the habitat type (Aarssen 2001). However, the general *shape* of the predicted relationship along these gradients defined by a

unimodal central tendency and particularly by the monotonic decreasing phase toward the highly fertile, undisturbed ends of the gradients on regional scales (Fig. 1g), is accounted for primarily, we suggest, by the two major variables on the habitat templet represented in Figs. 1c, f. Note also that species with relatively large size (characteristic of highly fertile, undisturbed habitats) may be associated with relatively small population sizes and longer generation times, resulting in higher probabilities of extinction and slower rates of evolution compared with smaller species (Tokeshi 1999), which may further limit species richness in highly fertile, undisturbed habitats.

Confounding interaction effects between habitat fertility and disturbance

Consistent with the predictions of other models (Huston 1979, 1994), dissecting these predicted patterns on each gradient separately (Fig. 3) illustrates that the hump-shaped pattern of resident species richness on habitat fertility gradients should be most prevalent across habitats that are all affected by a similarly *intermediate* level of disturbance (Fig. 3b). Patterns along a habitat fertility gradient may be undetectable if the habitats being compared all have very high disturbance levels (Fig. 3c), or if the habitats all have very low disturbance levels (Fig. 3a), despite, in the latter case, wide variation in community biomass or productivity (Fig. 3a). Likewise, the hump-shaped pattern of resident species richness on disturbance gradients should be most prevalent across habitats that all have a similarly *intermediate* level of substrate fertility (e.g. Dupre & Diekmann 2001) (Fig. 3e). Failure to detect any pattern of species richness variation across disturbance gradients (e.g. Mackey & Currie 2000) may, therefore, result from a failure to control for this potentially confounding effect of variation in habitat fertility. For habitat types with extremely high fertility, variation in disturbance level can produce an extremely wide gradient of community biomass or productivity (Fig. 3f), yet there may be no significant pattern of species richness along this gradient because of the uniformly low species pool size predicted for extremely fertile habitats, regardless of disturbance level (Fig. 3f). Hence, a given selection of habitats chosen intentionally to cover a broad gradient of community biomass or productivity on the habitat templet in Fig. 1g may represent wide (uncontrolled) variation on both the habitat fertility and disturbance gradients, yet none of these gradients independently may be associated with any significant pattern of variation in species richness, because the predicted effect of the habitat fertility gradient on species richness is completely confounded by the pre-

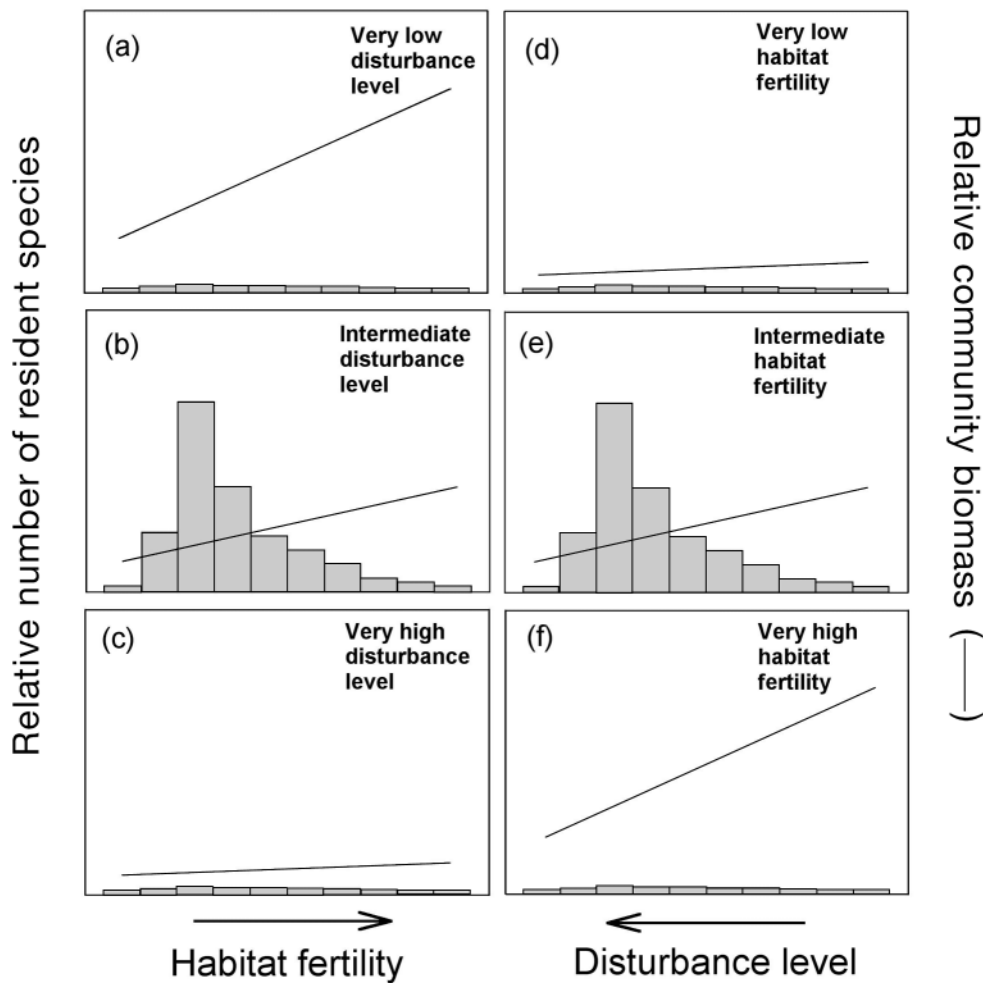


Fig. 3. The 'hump-shaped' pattern of predicted species richness variation (bars) on gradients of habitat fertility ('x-axis' in Fig. 1g) may be confounded by the level of disturbance (a, b, c). Similarly, the 'hump-shaped' pattern of predicted species richness variation on gradients of disturbance ('y-axis' in Fig. 1g) may be confounded by habitat fertility (d, e, f). Lines represent predictions for relative community biomass or vegetation productivity along each gradient (cf. main text).

dicted effect of the disturbance gradient (and vice versa). This may account, in some studies, for the absence of unimodal patterns (and in some cases, the absence of any significant pattern) in species richness along productivity gradients (see reviews by Waide et al. 1999; Mittelbach et al. 2001). This may also account for the fact that most declared hump-shaped distribution patterns are conspicuously hump-shaped only on the upper-bound line; i.e. whereas high species richness is restricted primarily to relatively low productivities, low species richness can occur at all productivities (Grace 1999), possibly, we suggest, because of confounding effects of uncontrolled covariation in habitat fertility and disturbance effects across sites.

Further complications arise from the fact that habitat fertility and disturbance level are not always entirely independent. Many disturbances that create new

habitats (e.g. volcanic activity, moraines from glacial retreat) are necessarily associated with nutrient-poor substrates. Some large scale disturbances from forces such as erosion, flooding, landslides and severe fires with wind blown ash can remove nutrients completely from one habitat and add them to another. Harvesting by humans (e.g. agriculture, logging) can also remove nutrients from a habitat, although nutrients may be returned with fertilizer application. Most other disturbances, however, (e.g. from windthrows, ice storms, ground fires, shoreline wave action, winds on sand dunes, animal grazing, burrowing and trampling, vehicle traffic, mowing and other activities of humans) affect only the balance of nutrient residency in the soil versus vegetation and do not result in any significant net change in the total ecosystem nutrient content of the habitat.

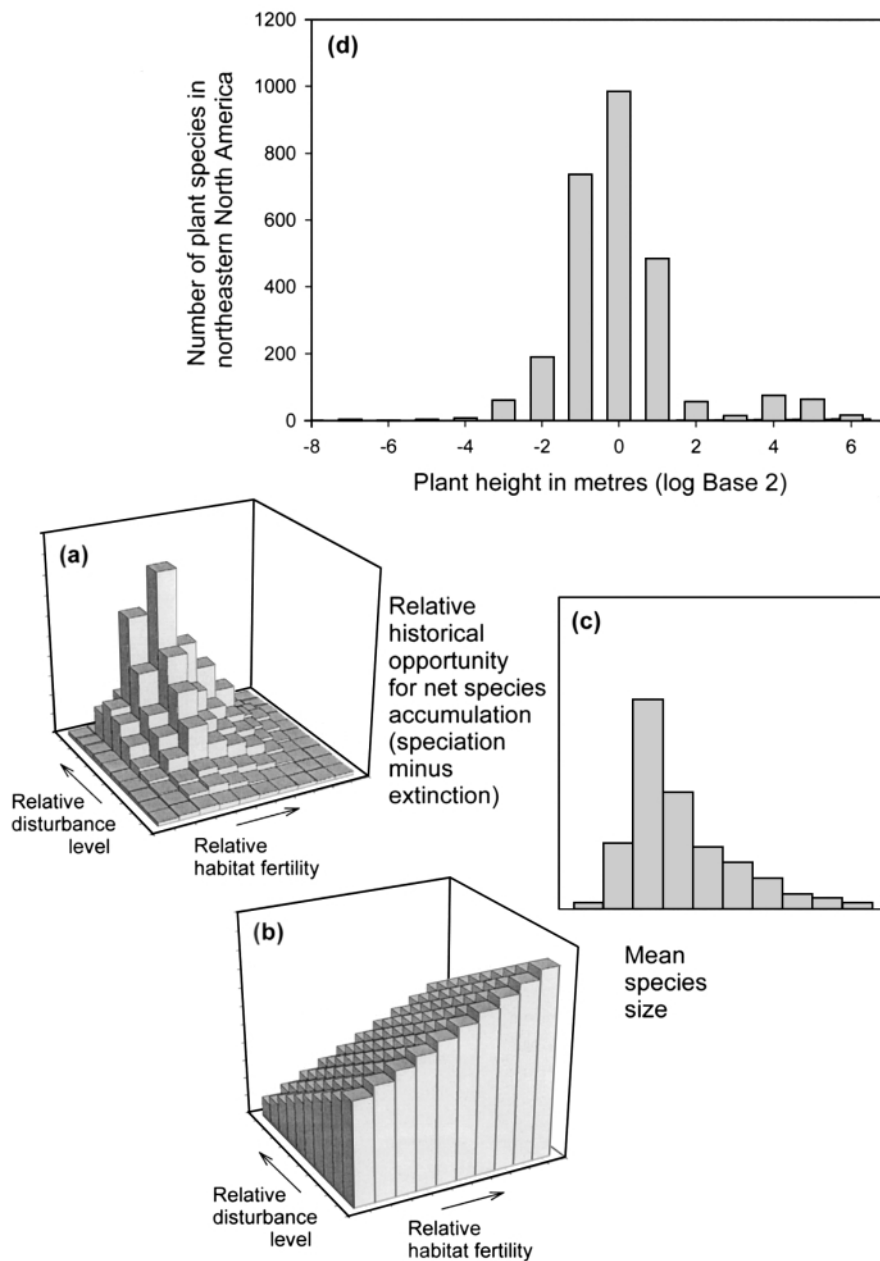


Fig. 4. A log-normal frequency distribution of species sizes across regional floras (c) can be predicted from the expectation that the largest plant species should be generally adapted (and hence primarily restricted) to highly fertile, undisturbed habitats (b) and that such species should be relatively few in number because of constraints on the relative historical opportunity for net species accumulation (speciation minus extinction) in highly fertile, undisturbed habitats (a). Support for this prediction is shown in the distribution of representative maximum plant heights recorded for the vascular plants of northeastern North America ($N = 2,715$ species) (d). Data are from Gleason & Cronquist (1991).

These problems of interpretation are exacerbated by the common practice of using the same units, i.e. community biomass, to measure the effects of both relative habitat fertility and relative disturbance level (e.g. Fig. 3). Measuring nutrient levels directly as units of habitat fertility is more time consuming and more expensive. These constraints may be at least partially overcome by using biological assays to measure soil fertility (e.g. Bell

& Lechowicz 1991; Richard et al. 2000). Measuring disturbance level directly on any kind of continuous scale, however, is even more problematic. Often, only qualitative categories can be assigned for comparing disturbance levels, e.g. presence/absence scores for indicators of disturbance from various sources. Practical limitations aside, however, long-term studies could be used to compare biomass production in enclosures pro-

tected from disturbance by wildlife and humans relative to biomass production within adjacent exposed vegetation to generate a unitless ratio as a continuous quantitative index of disturbance level from these sources. Time since the last major disturbance has also been used as a continuous quantitative index of disturbance level (e.g. Viswanathan & Aarssen 2000).

Predicting species size distribution across regional floras

If the historical opportunity for origination of adapted species has been greatest in habitats with some intermediate levels of both substrate fertility and disturbance (Figs. 1c, 4a) and if the sizes of species that are adapted to these habitats are also relatively intermediate in magnitude (Figs. 1d, 4b), then the distribution of species sizes across a regional flora can be predicted to be right-skewed unimodal (Fig. 4c). This prediction is supported by an analysis of plant height data for the vascular flora of northeastern North America where the right-skewed unimodal pattern displays, on a transformed axis, as a log-normal (base 2) distribution (Fig. 4d). This kind of body size distribution, with more species belonging to smaller size classes than to larger size classes, has been widely reported for animals, where the right-skewed pattern has been interpreted in terms of niche specialization, energetic and allometric constraints (Brown 1995) and the 'left wall' effect on organismal complexity (Gould 1988). The interpretation developed here for plants, however, represents an additional possible explanation derived from the species pool hypothesis applied to the habitat templet.

Conclusions and future directions

The species pool hypothesis predicts patterns in the distributions of species richness (Fig. 1g) and species size (Fig. 4c) in regional floras that are consistent with a growing body of data (e.g. Figs. 2, 4d). Searching for more direct evidence in support of this model will require research focus on several key questions: What is the pattern of historical habitat commonness variation on major environmental gradients (Fig. 1a)? To what extent is the relative opportunity for plant speciation in a given habitat type dependent on the historical relative commonness of that habitat type (Figs. 1b, c)? How does the distribution of mean sizes of adapted plant species along major habitat gradients (Fig. 1d) affect the relative number of adapted species containable per unit area along these gradients (Figs. 1e, f)? How are patterns of species richness variation across habitat gradients affected by interaction between variation in habi-

tat fertility and variation in disturbance level (Fig. 3)? Progress in researching these questions will be facilitated by further development and evaluation of techniques for measuring relative habitat fertility and relative disturbance level independently within vegetation, and by methods of analyses that take account of the effects of spatial scale (Huston 1999). The present model is applied explicitly to regional scales of variation in habitat fertility and disturbance where unimodal (humped) distributions of species richness variation are particularly common. Larger (continental/global) scale patterns are likely to be more difficult to interpret, where plant species richness variation across sites may also be a product of variation in historical frequencies of habitat fragmentation and reproductive isolation and the historical frequencies of allopolyploidy and adaptive radiation (Ricklefs & Schluter 1993; Aarssen 2001).

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