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Reply from A.R. Ennos

Cipollini and Schultz's letter highlights the pervasive effect of wind on numerous aspects of tree ecology. I feel their work also illustrates an important point to be borne in mind by ecologists when they work on the effect of the wind. It is not enough merely to show that plants that are subjected to wind or mechanical stimulation are different from totally unstimulated plants. The total lack of any mechanical stimulation is, after all, highly unnatural. It is also essential, as Cipollini and Schultz have done, to show that there is a graded response, in which plants subjected to higher and lower windspeeds or to wind for longer or shorter periods are different.

The fact that they have shown that the increased resistance to herbivores and pathogens

is accompanied by a greater degree of lignification may also be significant. There is growing evidence that mechanical toughness is an important defence of plants against both herbivory¹ and microbial decomposition². The increased resistance they have found may therefore have been mediated by the increased toughness which lignification confers.

A. Roland Ennos

School of Biological Sciences,
University of Manchester,
Oxford Road, Manchester,
UK M13 9PT

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An honorary non-flying mammal pollinator

Carthew and Goldingay¹ review non-flying mammals as pollinators and, in keeping with their goal, disregard bats. As an interesting extension to Carthew and Goldingay's review, however, it

might interest the reader that in New Zealand there is *Mystacina tuberculata*², a bat that can fly, but often crawls or runs about on the forest floor, where it eats invertebrates, flowers, fruit, possibly pollen, and pollinates *Dactyloctenium aegyptium*, an endangered endemic plant that lives parasitically on the roots of other plants³. Since this bat crawls and does not fly to the plant, the flowers of which it pollinates, there might be some justification to giving it an 'honorary' mention in a review on non-flying mammals as pollinators.

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V.B. Meyer-Rochow

Dept of Biology
(Section Animal Physiology),
University of Oulu,
SF-90570 Oulu, Finland

I.A.N. Stringer

Dept of Ecology, Massey University,
Private Bag 11222, Palmerston North,
New Zealand

Morphological approaches to measuring biodiversity

Kaustuv Roy

Mike Foote

Morphological diversity has the potential to provide a very useful biodiversity metric in that it emphasizes essential aspects of diversity that are not picked up by taxonomic or phylogenetic metrics. While morphological diversity metrics are used increasingly in paleobiological studies, quantitative data on the spatial distribution of morphology in modern ecosystems are scarce. The comparison between different aspects of diversity is often essential in understanding the processes underlying observed biodiversity patterns.

Kaustuv Roy is at the Dept of Biology 0116, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0116, USA (kroy@jeeves.ucsd.edu); Mike Foote is at the Dept of Geophysical Sciences, University of Chicago, 5734 S. Ellis Avenue, Chicago, IL 60637, USA.

While the need to quantify patterns of global biodiversity is urgent, the relative utility of various biodiversity metrics is often unclear¹. The most commonly used measure of biodiversity is taxon richness – the number of species (or higher taxa) present in an assemblage or a region. A number of recent studies have also used phylogenetic relationships to generate biodiversity indices that weight taxa, in part, by their genealogical distance

from other taxa^{1–4}. However, other aspects of biological variety, namely morphological and ecological diversity, have received relatively little attention in this context. We define morphological diversity as some quantitative estimate of the empirical distribution of taxa in a multidimensional space (morphospace) that has axes that represent measures of morphology. This definition of morphological diversity is different, both qualitatively

and quantitatively, from the estimates of relative morphological distance (based on explicit models of character change) that underlie the phylogenetic diversity metrics. While these different forms of diversity are certainly not independent, they are also not redundant enough that one can necessarily serve as a proxy for another^{1,5,6}.

Over the past few years, paleobiological studies have compared quantitative estimates of morphological and taxonomic diversity and have clearly shown that temporal trends in morphological diversity often do not match trends in taxonomic diversity. These discordances, rather than being random, have implications for underlying evolutionary mechanisms. However, quantitative data on geographic patterns of morphological diversity for most living taxa on a continental or global scale remain scarce, although a limited set of studies that do provide direct and indirect estimates of morphological diversity for living organisms show geographic trends. Quantitative data explicitly designed to assess the geographic distribution of morphological diversity should be useful for understanding the distribution of biodiversity in modern ecosystems.

How to measure morphological diversity?

One must contend with three related issues in assessing morphological diversity.

(1) At what taxonomic level should organismic morphology be sampled, and how should this sampling proceed? (2) Which traits should be measured or scored? (3) Given a sample of taxa and traits, how should the diversity of these traits among taxa be computed? These choices depend on the specific evolutionary and ecological questions at hand.

Sampling

In ecological studies of morphological diversity, how species are added to communities (for example, by increased niche packing versus an expansion of niche space) is often of interest⁵. Thus, the species is the obvious choice of sampling unit. At the other extreme, in macroevolutionary studies concerning the diversity among major body plans, higher taxonomic levels (e.g. classes) may be the sampling units. One example of this line of research concerns the morphological diversity of Cambrian versus Recent arthropods⁷.

Because species are nested within higher taxa, however, species-level sampling can also capture the differences among higher taxa⁸. Targeted sampling of single representatives of higher taxa has been criticized on the grounds that this may inflate the estimated dispersion among forms, and random sampling among species has therefore been advocated⁸. However, if the divergence among these body plans is of interest, and if there is a meaningful correspondence between higher taxa and body plans, sampling higher taxa may be justified^{1,7}.

Trait selection

Assessment of morphological diversity is underlain by the establishment of a morphological space (morphospace) that has axes that represent quantitative measures of morphology. Organisms present an indefinitely large number of potentially quantifiable traits, but in practice only a small number of features can be studied, whether with discrete or continuous variables. Therefore, we cannot strictly measure overall morphological diversity, but only diversity with respect to some set of traits. The robustness of evolutionary and ecological patterns can be assessed by determining whether different sets of traits yield similar patterns⁹. Ecomorphological studies tend to use characters known or presumed to be of functional or ecological significance (e.g. beak size in birds)¹⁰. An alternative is to seek broad coverage of morphology, measuring traits covering various aspects of the organism. Although the relationship among these two approaches has yet to be investigated in great detail, the ubiquity of character correlations¹¹ suggests that temporal and spatial patterns in the diversity of targeted and broadly

sampled traits may often agree. Once the relevant traits are chosen, many methods are available to quantify these traits¹²⁻¹⁴. These methods generally establish what are referred to as empirical morphospaces, those whose limits are determined by the taxa sampled. Some organisms, on the other hand, have forms that, at least if we are willing to simplify, can be placed within theoretical morphospaces that are underlain by simple generative or structural models. Some morphological parameters in such models have theoretical bounds, so that the total space does not depend strongly on the organism sampled (although the space *occupied* does). The most noteworthy case is that of coiled shells (e.g. Ref. 15).

Computing morphological diversity

The approaches just outlined yield an ordination of taxa in a multidimensional space. Two general classes of metrics have been used to compute morphological diversity from such ordinations: (1) those that measure the extent of morphospace occupation, and (2) those that measure pairwise differences among taxa. The term *disparity* has generally (but not exclusively)⁷ been used for measures of morphological diversity based on average morphological differences among taxa. In addition to diversity of form, patterns such as clustering in morphospace, measured with nearest-neighbor distance and related metrics, are often important in morphological studies^{5,10}.

The range (or its multivariate extensions such as volume), for continuous characters, is commonly used to express morphological diversity. For discrete characters, the number of character states or character-state combinations^{16,17} can be used. These measures have intuitive appeal, but suffer from a strong sample-size dependence. This problem is especially severe in studies in which we do not know how the number of taxa sampled relates to the true richness¹⁷. For this reason, some have advocated sample size-correction via rarefaction or simply using measures that do not depend strongly on sample size^{5,17}.

Variance (and its multivariate analog, mean squared pairwise morphological distance among taxa), for continuous characters, measures the dispersion among forms. This measure has been advocated for its relative insensitivity to sample size. Mean pairwise character difference^{5,12} plays a similar role for discrete characters, although other metrics based directly on character-state frequencies (e.g. Ref. 5) are arguably more appropriate¹⁸.

For any measure of morphological difference between species, the issue arises whether that distance should be taken at face value or somehow assessed in light of

evolutionary pathways^{3,19}. For studies that emphasize the functional role of convergent traits¹⁰, two taxa having the same value for a trait should be considered 'identical', even if each reached the state via a very different evolutionary pathway. On the other hand, if one is interested in total rates of morphological evolution, not simply the rate of accumulation of net differences, then it makes sense to allow reversals to contribute to measured character differences, even if little or no net change has occurred¹⁹.

While some theoretical morphospaces may accommodate a very wide range of taxa (e.g. Ref. 15), most schemes for measuring morphology greatly limit the taxonomic scope of ecological and paleontological studies²⁰. One would like, for example, to measure the disparity among all Cambrian animals in order to assess the pace of early morphological diversification, but we are far from having a meaningful set of traits that can be measured for all the known phyla (but see Ref. 16 for skeletonized phyla). Likewise, we would like to know whether the tropics or high latitudes systematically have higher morphological diversity, but we are confined to assessing the pattern in a particular higher taxon, say, birds. Taxonomic coverage can often be broadened by using discrete rather than continuous characters, but species in different phyla are still difficult to place in the same morphospace. This remains an important problem for future studies of morphological diversity.

Temporal trends in morphological and taxonomic diversity

Over the past few years there has been a renewed interest among paleobiologists in quantifying temporal trends in morphological diversity (e.g. Refs 17,21,22). Results from a number of different taxa, including trilobites^{6,21} and other arthropods⁷, gastropods²³⁻²⁵, blastozoan echinoderms²² and seed plants²⁶ have shown that trends in taxonomic diversity (i.e. number of species or higher taxa) and morphological diversity trends may be discordant, even if not completely decoupled. For some clades, morphological diversity increases rapidly at first, and then remains stable (or even decreases) while taxonomic diversity increases (e.g. Refs 6,26; Fig. 1a). For other taxa, morphological radiation continues late in the clade's history when taxonomic diversity shows a decline (e.g. Ref. 6; Fig. 1b). Discordances between taxonomic and morphological patterns, while sometimes counterintuitive at first glance, may be expected from theoretical considerations. For example, under simple time-homogeneous branching models, unconstrained morphological evolution yields a linear increase in morphological variance²⁷⁻²⁹. The pattern

seen in a number of clades, wherein the rate of increase in disparity slows during the course of an evolutionary radiation, suggests, among other possibilities, a temporal decline in the sizes of morphological transitions or taxonomic turnover rates²⁹. In some cases, these inferences of evolutionary mechanisms have been corroborated by detailed phylogenetic analysis (e.g. Refs 23,24,30). Early morphological diversification could conceivably reflect the use of characters that discriminate higher taxa, but one study⁹ showed that this pattern persists even when such characters are omitted. Several studies have also demonstrated consistent evolutionary patterns regardless of whether individuals, species or genera are the sampling units^{6,9,17}. With respect to a decline in diversity, an extinction event will tend to reduce the range of occupied morphological space. However, if extinctions were effectively random with respect to morphology, then variance could remain high as diversity declined, and a substantial reduction in variance could require the demise of an extremely large proportion of the standing crop of taxa^{6,31-33} (Fig. 2).

Morphological diversity trends in modern ecosystems

For most living taxa, we lack quantitative data on the spatial distribution of morphological diversity at continental or global scales. There is, however, enough evidence to suggest interesting spatial trends in morphological diversity. It has been argued that, for communities dominated by competitive interactions and saturated with species, increasing taxonomic diversity (i.e. addition of species) should lead to an increase in the total volume of occupied morphospace (e.g. Ref. 10). On the other hand, addition of species to other communities may simply involve insertion within the bounds of the existing morphospace, thereby keeping the total morphological volume constant¹⁰. A review of over a dozen different morphological studies of birds, bats, lizards and fishes revealed a general tendency for the total volume of morphospace to increase with diversity, although some studies showed no significant trends¹⁰. Nearest-neighbor distance within the individual morphospaces tended not to vary with the number of species. This suggests that species tend to be preferentially added to the periphery of the existing morphospace¹⁰. Similar patterns were also shown for a tropical-temperate comparison of night-flying moths⁵, with tropical faunas having a higher morphospace volume, but nearest-neighbor distances that were comparable with those in temperate faunas. Analyses such as these imply that the importance of tropical diversity often resides not

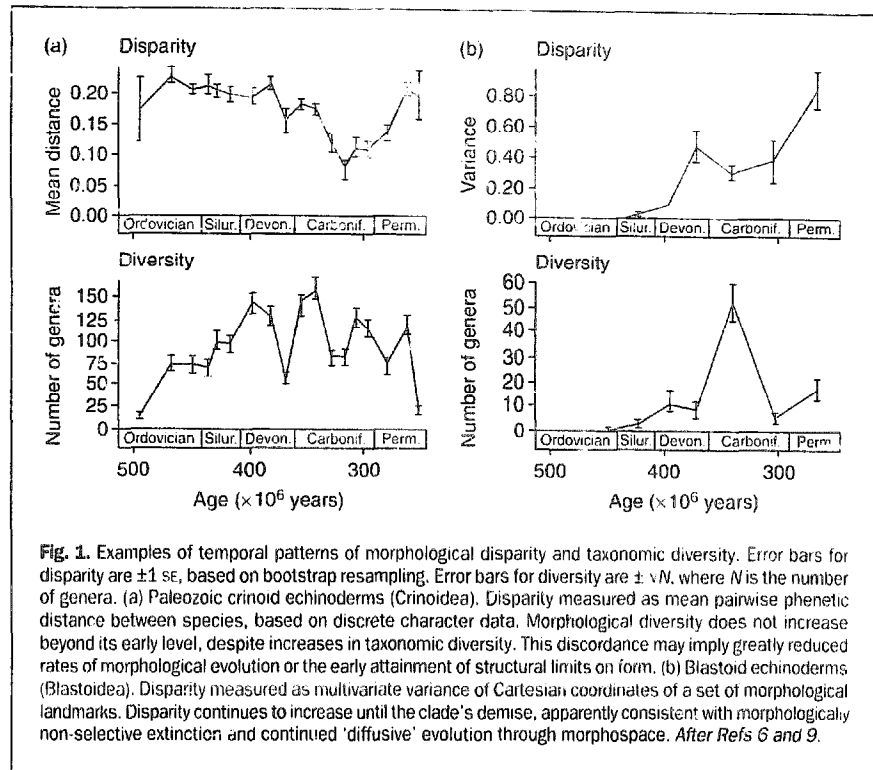


Fig. 1. Examples of temporal patterns of morphological disparity and taxonomic diversity. Error bars for disparity are ± 1 se, based on bootstrap resampling. Error bars for diversity are $\pm \sqrt{N}$, where N is the number of genera. (a) Paleozoic crinoid echinoderms (Crinoidea). Disparity measured as mean pairwise phenetic distance between species, based on discrete character data. Morphological diversity does not increase beyond its early level, despite increases in taxonomic diversity. This discordance may imply greatly reduced rates of morphological evolution or the early attainment of structural limits on form. (b) Blastoid echinoderms (Blastoidea). Disparity measured as multivariate variance of Cartesian coordinates of a set of morphological landmarks. Disparity continues to increase until the clade's demise, apparently consistent with morphologically non-selective extinction and continued 'diffusive' evolution through morphospace. After Refs 6 and 9.

simply in the number of species present but also in the greater diversity of form.

For marine faunas, quantitative data on spatial distribution of morphological diversity are even scarcer, but it is clear that temperate-tropical differences exist³⁴⁻³⁶. It has been shown that tropical marine communities contain novel morphologies that are absent from temperate and high-latitude faunas³⁵⁻³⁷, and the reverse is also undoubtedly true. Some have also suggested that tropical-temperate differences in polymorphism exist for marine molluscs³⁸. Many of the novel tropical molluscan morphologies appear to be antipredatory in function, and their evolution was arguably driven by increased predation pressure in the tropics³⁶. However, while the taxonomic differences between tropical and temperate assemblages can be readily quantified (e.g. Ref. 39), associated morphological differences have yet to be assessed. Such analyses are certainly needed (along with phylogenetic studies) for weighing the 'quality' of biodiversity against its 'quantity'³¹.

In addition to latitudinal patterns, for a number of taxa there also appear to be distinct differences in morphological diversity between continents and between oceans, but again quantitative data are scarce. Indications of regional differences in morphological diversity come from indirect evidence, namely discordances between species-level patterns and those seen at higher taxonomic levels. For example, plant species diversity in the phylogeographic region Malesia is less than half

that of the neotropics but Malesia contains more families^{39,40}. Given that higher taxa generally reflect greater morphological divergence than species do, this difference would seem to suggest that Malesia is morphologically more diverse compared with the neotropics, where diversity of lower taxa is greater³⁹. Similar patterns in the distribution of higher taxa exist for other groups (e.g. Ref. 41), but exactly how these translate into patterns of morphological diversity is currently unknown.

Morphological diversity as a biodiversity metric

Is morphological diversity a good metric for quantifying spatial patterns of biodiversity? We think that it is. For many people, morphological diversity is undoubtedly the most intuitive measure of biological variety (see Refs 1 and 4). Second, from a practical point of view, morphological diversity patterns (as defined here) are easier to compute than metrics that require an estimate of phylogeny¹⁻⁴, whether these metrics are based simply on cladistic rank², or character diversity as well³⁴. We also suspect - although this has not been studied in detail - that phylogenetic metrics, partly because they rest on genealogical estimates, and partly because some of them invoke models of character evolution (see Refs 3 and 4), are less stable than simple measures of morphological diversity. The contrast between phylogenetic and other metrics is especially relevant for large groups. Not only are robust phylogenies currently

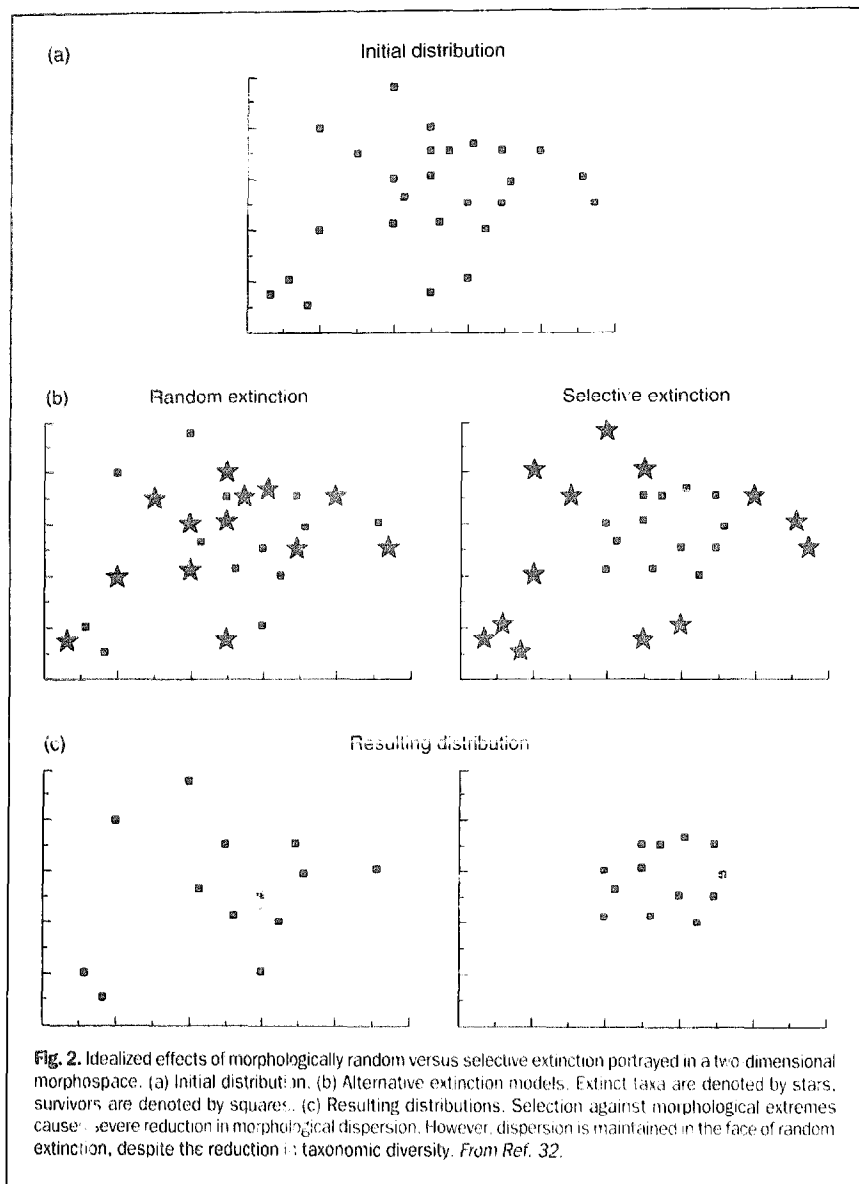


Fig. 2. Idealized effects of morphologically random versus selective extinction portrayed in a two dimensional morphospace. (a) Initial distribution. (b) Alternative extinction models. Extinct taxa are denoted by stars, survivors are denoted by squares. (c) Resulting distributions. Selection against morphological extremes cause severe reduction in morphological dispersion. However, dispersion is maintained in the face of random extinction, despite the reduction in taxonomic diversity. From Ref. 32.

unavailable for most large clades, but the number of equally supported alternative topologies increases with the number of taxa analyzed. Choosing among these and assessing the accuracy of the chosen phylogeny pose difficult problems⁴². This, however, is not to deny the utility of phylogenetic metrics; given accurate evolutionary trees, these metrics can evaluate part of the historical component of present diversity. Identifying areas with unexpectedly high (or low) morphological diversity for the number of species present could be useful for setting conservation priorities⁴³, and understanding the evolutionary and ecological basis of such anomalies through phylogenetic analyses would help us to understand the historical controls on biological diversity.

While it is clear that the distribution of species in morphospace is partially owing to their phylogenetic legacy, the question of how the occupation of morphological

space is constrained by phylogenetic structure has received less attention^{10,44} (but see Refs 24 and 30). It is worth reiterating that morphological and phylogenetic diversity metrics emphasize different aspects of biodiversity and one is not a proxy for the other, nor is either more fundamental. The distribution of taxa in morphospace reflects phenetic similarity (based on both primitive and derived characters), while the genealogy can be viewed as reflecting the 'routes of colonization' of that space⁴⁵. Finally, patterns of morphospace occupation, at some level, are controlled by functional and ecological attributes. Although these controls are complex and still poorly understood^{1,10}, they are nevertheless reflected in measures of morphological diversity.

In 1878, A.R. Wallace (Ref. 46, p. 121) wrote, 'Animal life is, on the whole, far more abundant and varied within the tropics than in any other part of the globe, and a

great number of peculiar groups are found there which never extend into temperate regions' (emphasis added), thus recognizing the distinction between taxonomic and morphological diversity patterns. Today, the shapes of latitudinal gradients in taxonomic diversity are known for many living organisms but quantitative data on morphological patterns remain scarce. From a biodiversity perspective, the effects of ongoing extinctions on taxonomic diversity are being quantified but their effects on morphological diversity remain virtually unknown³¹. For example, one could ask if there are differences in extinction susceptibilities of taxa residing in different parts of the morphospace (body size may be one such axis) or, conversely, if there are types of perturbations that tend to selectively affect certain portions of the morphospace³¹. Recent paleobiological studies have shown the utility of studying morphological patterns. In modern ecosystems, quantifying which combinations of traits occur where and how commonly is an important research agenda⁴⁷. Biodiversity metrics based on such data would nicely complement ongoing efforts to measure the phylogenetic components of biodiversity.

Acknowledgements

We thank D.J. Miller and T. Price for discussions and comments, and D. Schluter, P.H. Williams and an anonymous reviewer for helpful reviews.

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