PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

Ecological Correlates of Plant Range Size: Taxonomies and Phylogenies in the Study of Plant Commonness and Rarity in Great Britain [and Discussion]

Colleen K. Kelly, F. Ian Woodward and M. J. Crawley

Phil. Trans. R. Soc. Lond. B 1996 **351**, 1261-1269
doi: 10.1098/rstb.1996.0109

Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain

COLLEEN K. KELLY[1]* AND F. IAN WOODWARD[2]

[1] *University of North Texas, Denton, Texas 76203–5218, U.S.A.*
[2] *Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN U.K.*

SUMMARY

Recent simulations have shown that the lack of resolution to be found in taxonomic relative to phylogenetic classification systems only slightly inflates the probability of Type 1 error (inappropriately rejecting the null hypothesis) in evolutionary comparative studies that take relatedness into account. Thus, on this basis, taxonomies may be expected to organize the data adequately for such studies when phylogenies are not available. However, phylogenies instigate particular rearrangements in plant classification that are not easily addressed by simulation, and an analysis of specific variables is used here to gain insight into the consistency of results when a large dataset is organized prior to analysis first with a taxonomy, and then with a phylogeny.

This study examines commonness and rarity as it is measured by plant range size of species drawn from the floras of the islands of Great Britain and Crete. The data were restricted to native species of the main island of each group. Using a taxonomic classification of the data, both floras were investigated for the effect of range size on woodiness versus non-woodiness, and tree versus shrub life form. The flora of Great Britain was further examined for possible differences in range size due to overall plant size, and pollination and dispersal types. Using a phylogeny to organize the data, all of the same comparisons of growth form and mutualistic interactions were made for the flora of Great Britain, plus comparisons of cloning versus non-cloning, vining versus non-vining and reproductive schedule (annual, biennial and perennial).

Although a phylogeny is the preferred tool for organizing that data, the results suggest that analyses using a taxonomy can lead to conclusions reliable across classification schemes. With either organizational system, trees had larger range sizes than shrubs, and wind-pollinated species had larger range sizes than related non-wind-pollinated species. Additional analyses also indicated that non-clonal plants are more widespread than related clonal species. Changes in the relative position and number of contrasts within comparisons indicate that the exact effect of using a phylogeny versus a taxonomy will depend on the distribution within the phylogeny of the trait being studied.

1. INTRODUCTION

According to a commonly used textbook, ecology is the study of the 'distribution and abundance of organisms' (Krebs 1994), i.e. the study of commonness and rarity among and within species. Since Krebs first elevated this definition to prominence in 1972, ecological studies have included functional aspects of organisms not directly determining distribution or abundance of species, as can seen by a casual perusal of ecological journals. Nonetheless, inherent in the majority of ecological studies is an underlying assumption that the focal property or response has a role in determining the geographical extent or local abundance of the study organism(s). In addition to this central role in basic ecology, the potential relationship between species abundance or distribution and the probability of extinction has generated a flurry of research in conservation biology. The literature on the study of commonness and rarity in both basic and applied ecology is ably reviewed by Gaston (1994), providing a current, comprehensive guide to the topic.

Unfortunately, few of the plethora of studies on commonness and rarity have taken into account the potentially confounding effect of phylogenetic relatedness (but see Gregory *et al.* 1991; Pagel *et al.* 1991; Kelly 1996), although evidence suggests that relatedness is likely to be of general importance in determining range size (Hubbell & Foster 1986; Maurer 1991). That is, in the search for causes of similarity among species in commonness or rarity, the possibility that species may be similar due to common ancestry, rather than or as well as ecological pressures, has largely been ignored. Such oversight is a cause for some concern; simulation studies have shown that inappropriately treating species as independent data points and ignoring the effect of phylogenetic relatedness on interspecific similarity results in a one in three chance of showing an ecological or functional relationship between variables when none actually exists (Martins & Garland Jr. 1991; Harvey & Pagel 1991; Purvis *et al.*

---

* Present address: Department of Zoology, Oxford University, South Parks Road, Oxford OX1 3PS, U.K.

Phil. Trans. R. Soc. Lond. B (1996) **351**, 1261–1269
Printed in Great Britain

1994). In the study reported here, we have used evolutionary comparative methods accounting for the effects of species relatedness in order to determine ecological correlates of plant commonness and rarity as measured by geographic range size.

The term 'commonness and rarity' may refer to the abundance or distribution of a species, or some combination of abundance and distribution (Reveal 1981; Brown 1984, 1995; Anderson 1985; Rabinowitz *et al.* 1986; Gaston 1994, 1996); herein we have focused on that aspect of commonness and rarity entailed in variation in species distribution. Until recently, the possible causes and effects of variation among species in geographic range size has received much less attention than have the possible causes of species abundance distributions (Gaston 1996). The emerging interest in range size may be attributed to increasing awareness that regional scale phenomena may pinpoint or feed back to local ecological effects in a manner not necessarily predictable from study of a phenomenon at a local level (Lawton 1990; Gaston 1994; Brown 1995). We note also, however, that while the present study examines distribution alone, the repeated demonstration of a positive relationship between range size and intraspecific abundance (e.g. Hanski 1982; McCoy 1990; Obeso 1992), indicates that the results reported here may have import for the study of species abundances.

Range size may also indicate the ecological flexibility of a species (Brown 1984, 1995). It has been correlated with the number of habitat types and/or the scope of a particular environmental variable that a species can withstand (e.g. Glazier 1980; Thomas & Mallorie 1985; Pagel *et al.* 1991), and has been assumed thereby to suggest the ability of a trait to confer resistance to environmental change or variability in either space or time. Previously, Kelly (1996) used this logical relationship between range size and environmental flexibility to identify plant functional types (PFTs). PFTs are proposed to be identifiers of generalized vegetation groups, such that the effects of environmental change on vegetation can be predicted through simulation modelling without having to resort to the impracticable course of describing the natural history of every plant species in a region. The search for such identifiers is driven by the concept that there are attributes of plant species that can be used to place a species in an inclusive group whose members will respond similarly, or be similarly sensitive, to environmental perturbation.

The study reported here is also novel in having examined the differences in results produced when the data are organized with phylogenies derived from cladistic techniques versus patterns produced when a traditional taxonomy is used to organize the data. Until recently, taxonomies were the only phylogenetic schemes available for evolutionary comparative methods in the inference of ecological (functional) relationships, and several studies have argued that without a fully resolved phylogeny a cross-species analysis is more appropriate than an analysis taking relatedness into account (e.g. Hammond & Brown 1995). However, Purvis *et al.* (1994) have shown that when the 'true' evolutionary tree is known, the use of an unresolved phylogeny such as is represented by a taxonomy only slightly inflates the probability of finding a pattern when none exists (the α value increases from 0.05 to 0.068). Even so, the efficacy of classical taxonomies may still be an issue: cladistically-derived phylogenies of the flowering plants have shown what appears to be a significantly different evolutionary map of relatedness among higher groupings within the Kingdom Plantae (Chase *et al.* 1993; Nickrent & Soltis 1995) than that produced by traditional taxonomic assumptions. The potential effects of these differences may have relevance to studies of the many groups of higher plants for which only taxonomies are available, as well as to previous comparative studies using taxonomies (e.g. Kelly & Purvis 1993; Kelly & Beerling 1995; Woodward & Kelly 1995). For this reason, we have used this opportunity to view the results reported here as a case study pointing to the effects these striking differences between evolutionary hypotheses (i.e. the traditional taxonomy versus the cladistically-derived phylogeny) can have on the results of evolutionary comparative analyses. The large size of our dataset is such that some of the potential problems of such a case study approach may be more easily avoided here than elsewhere.

2. MATERIALS AND METHODS

Although biologically speaking the terms rarity and commonness represent two ends of a continuum of distribution, species commonness or rarity are sometimes studied as categorical properties, particularly in reference to rarity. As Gaston (1994) points out, legal and conservation concerns may dictate such categorization for particular cases. However, because the research presented in this study aims to determine basic ecological properties of plant range size, commonness and rarity will here be treated as a continuous variable. Note, however, that commonness and rarity is the dependent variable, i.e. that which must be explained.

Range sizes had been determined for all possible species of the British flora according to Perring & Walters (1982) for Kelly (1996). Using only data from post-1930 collections, range size was calculated as the number of vice-counties (out of a possible 113) in which a plant appeared on the island of Great Britain (England, Scotland and Wales). Ecological information on the 1196 British plant species was drawn from Clapham *et al.* (1987).

For the flora of the island of Crete (Turland *et al.* 1993), range size had been assessed as the number of 10 × 10 km quadrants (out of a possible 158) on the main island from which a species had been collected since 1930. Ecological data were drawn from Tutin *et al.* (1993) for the 1084 plant species. Non-native species were excluded from analyses, and the data were restricted to dicotyledonous plants.

To determine the correlates of plant range size in the previous study, where a taxonomically derived tree had been applied (Kelly 1996), the main island of Great Britain (England, Scotland and Wales) and the main island of Crete had been chosen because (1) islands provide an unequivocal delimitation of an area; (2) each of these two particular floras has reliable distributional information for absence as well as presence of plant species within each geographical subunit; and (3) the two provide a comparison of a potentially important ecophysiological factor, i.e. water availability. For each island, it was assumed that all species are subject to the same set of physical factors affecting distribution. Within each island, it may be inferred that different 'choices' (relative range sizes) are due to different capabilities or biological interactions, rather than, for example differential availability of geographical areas in which to expand, as can be the case when comparing species from different regions (Letcher & Harvey 1994), or differences in the physical or climatic conditions. The phrase 'plant range size' will be used here to refer to the areal extent of species within one of the two designated islands.

(*a*) *Comparative methodology*

The evolutionary comparative methods of Pagel (1992) and Purvis (1992) are derived from Felsenstein (1985), and are based on the idea that the important information in demonstrating a functional relationship is the changes in the branches of a classificatory 'tree' that has been constructed with the available data (cf. Ridley 1983). Previously, the evolutionary 'trees' had been constructed using Cronquist (1981), one of the most widely used classification systems (Kelly 1996). In the new work reported here,we used the phylogenies of Chase *et al.* (1993), and Nickrent & Soltis (1995) to determine the evolutionary relationships among species; Thorne (1992) was used to clarify relationships among families and subfamilies where this information was not available from the phylogenetic treatments directly. Further description of the methodology is available in papers cited above.

For the analyses using taxonomies, the categorical variables inspected as potential determinants of plant range size in Great Britain or Crete were woodiness versus non-woodiness, trees versus shrubs, trees versus herbs and shrubs versus herbs; all variables were examined for each flora separately. For the British flora alone the effects of wind versus non-wind pollination, self- versus animal pollination, and dispersal type on range size were also investigated. Wind-pollinated species were excluded from the data prior to comparisons of range size in self- versus animal pollination.

For the analyses using phylogenies, we examined for Great Britain alone all the factors listed in the previous paragraph, additionally investigating the effects of reproductive schedule (annual, biennial or perennial), cloning and vining on range size. The analyses using the cladistically derived tree were performed using CAIC, as described in Purvis & Rambaut (1995).

(*b*) *Identifying taxonomic patterns*

We also applied a nested analysis of variance (ANOVA) with unequal sample sizes (Sokal & Rohlf 1995) to the taxonomic structure of each of the two data to describe how variation among species in a continuous character such as range size may be distributed among taxonomic levels (Harvey & Mace 1982; Clutton-Brock & Harvey 1984). Levels which account for a large or significant proportion of the total variance indicate that the distribution of the value of the target variable differs among the taxonomic groups comprising that level, and each group at that level may be examined for within-group patterns in the target variable relative to a selected ecological factor (e.g. Woodward & Kelly 1995).

Unfortunately, nested ANOVA is subject to two caveats here. First, the results of a nested ANOVA of this sort of data can be significantly influenced by small changes in the data included in the analysis, even when the dataset would normally be considered relatively large (e.g. 350+ species; Kelly 1996). Second, although the structure of a taxonomic classification scheme lends itself well to the structure of a nested ANOVA, that of a cladistically derived phylogeny does not. Further, differences between either Cronquist (1981) or Thorne (1992) taxonomies and the phylogenies that have been published recently make the findings from a nested ANOVA of a taxonomically classified dataset only remotely transferable to the true phylogeny. This last observation points out a conflict in the dual recommendations by Silvertown & Dodd (this issue) that (1) only phylogenies be used in comparative analyses, and (2) nested ANOVAS first be performed to determine if significant variation in the target variable can be explained by higher organizational levels.

3. RESULTS

In analyses using taxonomies, two factors had been identified as significant determinants of relative range size (table 1). For plant species on the island of Great Britain, trees had greater range sizes than shrubs significantly more often than expected by chance ($n = 172$; 11 contrasts/2 disagreements; $p = 0.033$) and wind-pollinated species had greater range sizes significantly more frequently than non-wind-pollinated species ($n = 772$; 13 contrasts/2 disagreements; $p =$

Table 1. *Summaries of the analyses of ecological factors having a potential effect on plant species range size when a taxonomy is used to construct the 'tree'*

('Hypothesis' refers to the expected direction of difference in range size associated with the two categories. Significant level derived from one-tailed sign tests; * signifies $p < 0.05$. From Kelly 1996.)

hypothesis	Great Britain	Crete
woodies > non-woodies	25/11	59/26
trees > shrubs	11/2*	9/5
trees > herbs	7/2	
shrubs > herbs	24/12	
wind- > non-wind-pollinated species	13/1*	
outcrossed > self-pollinated species	15/7	
animal-dispersed > non-animal-dispersed species	37/17	

Table 2. *Results of nested analyses of variance of range size for the floras of Great Britain and Crete*

(Datasets were restricted to native species occuring only on the main island of each group. Range size values were log-transformed prior to analysis.)

	Great Britain		Crete	
taxonomic level	*p* value	% variance explained	*p* value	% variance explained
subclasses	< 0.01	11	< 0.0001	4
orders within subclasses	> 0.05	11	> 0.75	0
families within orders	> 0.25	0	> 0.25	0.1
genera within families	< 0.001	9	< 0.0001	15
error (species within genera)		69		81

Table 3. *Independent contrasts based on a phylogenetically organized dataset*

(An * is used to emphasize a comparison with significant differences between categories in range size. All patterns reported are for native species recorded on the island of Great Britain. Range size is measured as the number of vice-counties in which a species has been recorded during the period from 1950 to the present.)

hypothesis	no. of species	no. of disagreements/ total no. of contrasts	*p* value (1-tailed)
lifeform			
woody > non-woody plants	1196	23/42	0.323
trees > shrubs*	187	2/14	0.006
trees > herbs	1075	2/8	0.145
shrubs > herbs	1172	22/44	0.440
unitary > clonal*	1178	38/108	0.003
lianas > non-lianas	1125	6/20	0.058
pollination type			
wind > non-wind pollination*	788	2/12	0.019
wind > non-wind pollination (w/o trees)*	764	2/12	0.019
self- > animal pollination	742	16/38	0.127
dispersal type			
animal > wind dispersal	789	4/13	0.133
birds > other animal dispersors	402	4/13	0.133
reproductive schedule			
polycarpy (perennials) > monocarpy (annuals + biennials)	1196	61/118	0.323
polycarpy (perennials) > monocarpy (biennials)	936	29/51	0.201
multiple (biennials) > single season(s) (annuals)	358	10/24	0.271
multiple seasons, polycarpic > single season, monocarpic	1054	45/89	0.50

0.002). There were no differences in range size for any of the factors examined in the analyses of Cretan species. For the tree/shrub comparison of British species, 3 of the 11 contrasts were among taxa at or above the family level; for the comparison between wind- and non-wind-pollinated species, 7 out of the 13 comparisons were above the family level. These two distributions of contrasts did not differ from one another ($\chi^2 = 0.906$; $p > 0.3$).

The nested ANOVA showed that genera within families and subclasses explained significant levels of variation both for the 1196 species of the British flora, and for the 1084 species of the Cretan dataset (table 2).

In the analyses using a cladistically derived classification scheme, three factors were found to have a significant effect on range size (table 3). Wind-pollinated species had greater range sizes than non-wind-pollinated species, trees had greater range sizes than shrubs, and non-cloning species had larger range sizes than cloning species. Determining the possible interaction of trees and wind pollination was not possible using the preferred method of Read & Nee (1995), because of the few lineages in which trees occurred in this dataset (three), but analysis of wind pollination in which trees were excluded from the dataset also indicated that wind-pollinated species have larger range sizes than non-wind-pollinated species.

4. DISCUSSION

(*a*) *Phylogeny versus taxonomy*

Given the need to account for relatedness noted in the Introduction, but a lack of cladistically derived phylogenies with which to do so, is it valid to use taxonomies instead? The comparison of the results reported here, with those of Kelly (1996), indicate that analyses using taxonomies can show patterns similar to those of analyses using a cladistically derived phylogeny to construct an evolutionary tree. However, there are also other considerations supporting the use of taxonomies where phylogenies may not be available.

(*b*) *Practical reasons why a taxonomy may be sufficient when no phylogeny is available*

For many datasets, the lack of resolution offered by taxonomies relative to cladistic phylogenies will not be an issue. The results of Purvis *et al.* (1994) show that the probability for an independent contrasts analysis of falsely finding a significant relationship between x and y (a Type 1 error) using a poorly resolved classification scheme changes slightly from the conventionally acceptable $\alpha = 0.05$, to $\alpha = 0.068$ when branch lengths are assumed to be equal, which is the currently recommended procedure when branch lengths are unknown. The probability of determining that the data do not support the conclusion of a significant relationship when one actually exists (a Type 2 error) is also slightly inflated, but compares favourably to similar values for cross-species analyses, where the chance of a Type 1 error is 0.312. It is also worth noting that the probability of a false negative depends upon the probability of a false positive. Thus, from Purvis *et al.*'s (1994) figures, the chance that an independent contrasts analysis will inappropriately reject a relationship found using cross-species analysis is within the conventionally accepted range of values (Sokal & Rohlf 1995).

As a second practical consideration, in examining the effects of lack of phylogenetic resolution, Purvis *et al.* (1994) investigated the effect only of continuous variables, in which case the groupings at a node are determined by the values for that variable held by the taxa at that node in the dataset. When the independent variable is categorical, however, the groups are defined by the two states of the target variable. In many instances, the categorical variable has been one of fairly large import, such as major changes in habitat use (Kelly & Purvis 1993; Kelly 1995*b*; Kelly & Woodward 1995) or life form (Kelly & Beerling 1995; Kelly 1996). With such categorical variables, we would expect a greater likelihood that the independent variable defines real islands of relatedness than would be the case with continuous variables, and should be less vulnerable to any potential lack of resolution. Nonetheless, it would be helpful to know with certainty if the effects of lack of resolution on the probability of inferring a relationship where none exists is as small for categorical as it is for continuous variables.

Lastly, although the taxonomy may be highly unresolved, the data may not be. In the dozen or so datasets I have analysed using taxonomies, the total number of taxa at any node usually has not been especially high. With few taxa per node, the chance of incorrectly determining most-closely-related taxa decreases, the appropriate taxa will necessarily be compared in any one contrast, and inflation of either the α or β value will not be an issue.

(*c*) *Conceptual issues regarding taxonomies versus phylogenies*

A larger question in the issue of taxonomies versus cladistic phylogenies is how particular changes wrought by phylogenies will affect conclusions drawn from analyses using taxonomies. It is this question that the size, phylogenetic scope and history of the dataset discussed here offer a unique opportunity to examine. The cladistically derived phylogenies relevant to these data were applied primarily to relationships above the family level. Of interest, then, are the comparisons between trees and shrubs and between wind- and non-wind-pollinated species, where a large proportion of contrasts were above the family level. The pattern of greater range size in wind-pollinated species found with the original taxonomically based analysis is upheld in the analysis using a phylogenetic scheme. Similarly, the tree/shrub comparison showed significant differences between the two growth form categories when using a cladistically derived classification, as it had with taxonomically organized data. The analyses were affected by the changeover from taxonomic to phylogenetic classifications, however; both comparisons changed in the total number of contrasts found. The number of contrasts in the tree/shrub comparison increased, a result expected from the greater resolution of the phylogeny relative to the taxonomy. However, the comparison of pollination modes decreased in number of contrasts, although a greater number of contrasts were above the family level, where resolution increased, than for the tree/shrub comparison. The differences in the effects of systematic reorganization for the two comparisons illustrates the specific concern present when taxonomies are used, and that is unlikely to be revealed by simulation alone. That is, the impact of a cladistic rearrangement of a taxonomy on a comparative analysis depends upon the trait being studied. The cladistic restructuring had a dramatic effect on the Hammamelidae and Dilleniidae, where many trees are classed. Wind pollination proves through inspection of the data to have been more broadly distributed among groups than was 'treeness', and thus not so specifically affected by the restructuring of relationships in the cladistic analysis.

(*d*) *Ecological inferences*

When the greater range size of wind- versus non-wind-pollinated species seen here was revealed in the earlier analysis using a taxonomic classification system, Kelly (1966) proposed that the pattern demonstrated a previously unsuspected 'cost of mutualism'. The specificity of pollination, where only one or a very few animals can pollinate a species effectively, dictates that movement into a new habitat type or area is dependent on meeting the ecological demands of two or more species, i.e. both plant and pollinator species. The analyses performed here also indicate that the significant effect of wind pollination on range size is not a function of the significant effect of life form, as might be expected from the impression that many wind-pollinated species are trees; wind pollination was linked to greater range size whether or not trees were included in the data. Of interest in the analyses reported here, as in the earlier study, is the observation that when relatedness is taken into account, dispersal type shows no such dependence on animal vectors. The results of the analyses reported here support the earlier conclusion that animal dispersal, being a much 'looser' interaction than pollination (Wheelwright & Orians 1982), does not so restrict the ability of a plant species to move into a new habitat or area. Because a much greater number of animal species can disperse any single plant species, and many plant species can provide acceptable fruit to any one animal species, there is a high probability that any new habitat or area will provide an effective *in situ* dispersal agent for an invading plant species. Thus, in considering the effect of propagule dispersal type on range size, effective movement of a plant species into a new area needs to meet the ecological requirements of only one species for colonization by the plant, and should not as greatly affect range size as does pollination type.

A marked pattern in the results showed non-cloning species to have greater range sizes than cloning species. A common explanation for the high proportion of cloning species (up to 90%, and generally not less than 30–40%, of any flora examined; Kelly 1995*a*) is that cloning confers the ability to respond to habitat heterogeneity, and to 'smooth out' the effects of patchiness through averaging out the good and bad patches an individual encounters over its lifetime (Hartnett & Bazzaz 1983, 1985; Alpert & Mooney 1986; Alpert 1989, 1991). This explanation suggests that cloning species are better able to withstand the ubiquitous ecological variable patchiness, than are non-cloning plants. A logical conclusion of this hypothesis is that cloning species should be more robust and therefore more widely distributed, yet they are not. Although the general pattern shown in this study is not consistent with this explanation, it is a pattern consistent with experimental work using *Cuscuta europaea*, dodder (Kelly 1994). Based on this work, it has been proposed that the adaptive value of particular cloning responses can be gauged only in the context of particular schedules of patchiness (Kelly 1994). For example, forming short internodes between mother and daughter ramets when a mother ramet is in a rich patch has been proposed as the adaptive response to encounter with a rich patch (Sutherland & Stillman 1988; Cain 1996). However, this will not increase the probability of a daughter ramet encountering a rich patch if the patch is only large enough to hold a single ramet; indeed, such a response in this situation will in fact decrease the probability that a daughter ramet will encounter a rich patch (cf. Rubin 1987). In the estimation of adaptive value for this particular trait, the crucial variable is ramet size relative to patch size, and the situation described above is easy to imagine if we remember that a substantial number of clonal species have very large ramets, e.g. aspens and alders. However, the necessity of considering the environmental context holds, regardless of the absolute size of any one ramet. Work begun at Oxford in 1988 has shown that lineages within a species exhibit site-dependent response and branching patterns that appear adaptive relative to the resource regime from which the lineage is derived, as predicted by foraging theory developed to describe resource acquisition behaviour in animals (Charnov 1976; C. K. Kelly unpublished data). We suggest that the natural inference here is that any one lineage may be well suited to deal with a particular habitat, but the response schedule of that lineage may equally serve to decrease the success of colonization of a new habitat or area. Thus, and as observed here, clonal species would be expected to be potentially more vulnerable to environmental change, and less widely distributed than related non-clonal species.

As noted above, the results reported here showed the same difference between trees and shrubs in range size in Great Britain as that found in an earlier study (Kelly 1996). In the earlier paper, noting that Crete, with its dry Mediterranean climate, showed no difference between tree and shrub range sizes, Kelly proposed that when low water availability is not an environmental factor, trees might be expected generally to have greater range sizes than shrubs due to the competitive advantage conferred by greater height. Although the competitive advantage of trees has been suggested from individual experiments and theoretical treatments (e.g. King 1990) this has not previously been shown to have a general effect at higher levels of ecological organization such as that seen here.

For vines and non-vines, the reclassification of a single contrast from disagreement to agreement (observed 6 out of 20) would lead to the observation of significant differences in range sizes of vining versus non-vining species, as would the addition of a single supporting contrast. We therefore hesitate to draw any conclusions at this point, and would prefer first to examine additional data from Great Britain and additional areas, including those where the ecological role of vining may differ from that in Great Britain.

Finally, the lack of a significant result in an analysis may be as revealing as its presence. In our analyses, where phylogenetic relatedness is taken into account, dispersal mode did not predict range size. However, in previous studies where relatedness was not accounted for, range size has been found to be limited by dispersal ability (e.g. Carter & Prince 1985; Lawton & Woodroffe 1991; Primack & Miao 1992), as it has when studies have been limited to taxonomically defined assemblages (e.g. Hansen 1980; Juliano 1983; Kavanaugh 1985; Söderström 1989; Oakwood *et al.* 1993). Although the signficant results for taxonomically restricted studies appear to contradict the lack of pattern found in our larger study, which took relatedness into acccount through independent contrasts analysis, these differences are consistent with the significant variation in range size found at levels above that of species (table 2); significant variation in a nested ANOVA for higher levels of taxonomic organization indicates that ecological effects active within one taxonomic group are not necessarily the same as those operating across groups (Harvey & Mace 1982). Thus, the observation of a significant effect of dispersal on range size seen in previous studies may be attributable to sampling regime, as a relationship particular to the group being studied, or, in the case of cross-species analyses, unrecognized taxonomic biases in the dataset. Reproductive mode, which was categorized in the commonly used manner of annual, biennial (monocarpic) or perennial, also did not translate into differences in commonness and rarity when relatedness was taken into account, nor did comparisons between life forms other than trees versus shrubs. Of potential importance in their own right (e.g. Harper 1979; Hodgson 1986; Karron 1987; Longton 1992), both reproductive mode and life form are linked directly or indirectly to longevity and above-ground body size (in terms of either individual biomass or height), which variables might be expected to affect range size (Van Valen 1973, Aizen & Patterson 1990, Oakwood *et al.* 1993) yet they did not do so here.

In summary, the results discussed here suggest consequences of local effects not previously generally suspected (cost of mutualism; local adaptation by cloning plants), and possible reinterpretation of earlier results (the effects of dispersal). We are not alone in continuing to advocate the use of analyses that take phylogenetic relatedness into account in the search for ecological correlates of range size or any other biological trait, and emphasize that the application of such methods need not wait on the emergence of a definitive, cladistically derived phylogeny to be valid.

REFERENCES

Aizen, M. A. & Patterson, W. A. I. 1990 Acorn size and geographial range in the North American oaks (*Quercus* L.). *J. Biogeog* **17**, 327–332.

Alpert, P. 1989 Translocation in the nonpolytrichaceous moss *Grimmia laevigata*. *Am. J. Bot.* **76**, 1524–1529.

Alpert, P. 1991 Nitrogen sharing among ramets increases clonal growth in *Fragaria chiloensis*. *Ecology* **72**, 69–80.

Alpert, P. & Mooney, H. A. 1986 Resource sharing among ramets in the clonal herb *Fragaria chiloensis*. *Oecologia* **70**, 227–233.

Anderson, S. 1985 The theory of range-size (RS) distributions. *Am. Mus. Novitates* **2833**, 1–20.

Brown, J. H. 1984 On the relationship between abundance and distribution of species. *Am. Nat.* **124**, 255–279.

Brown, J. H. 1995 *Macroecology*. University of Chicago Press.

Cain, M. 1996 Spatial models of foraging in clonal plant species. *Am. J. Bot.* **83**, 76–85.

Carter, R. N. & Prince, S. D. 1985 The geographical distribution of prickly lettuce (*Lactuca serriola*). I. A general survey of its habitats and performance in Britain. *J. Ecol.* **73**, 27–38.

Charnov, E. L. 1976 Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* **9**, 129–136.

Chase, M. W. *et al.* 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastic gene rbcL. *Annls Missouri Botanical Garden* **80**, 528–590.

Clapham, A. R., Tutin, T. G. & Moore, D. M. 1987 *Flora of the British Isles*, 3rd edn. Cambridge University Press.

Clutton-Brock, T. H. & Harvey, P. H. 1984 Comparative approaches to investigating adaptation. In *Behavioural ecology: an evolutionary approach*, 2nd edn (ed. J. R. Krebs & N. B. Davies), pp. 7–29. Oxford: Blackwell.

Cronquist, A. 1981 *An integrated system of classification of flowering plants*. New York: Columbia University Press.

Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Gaston, K. 1994 *Rarity*. London: Cambridge University Press.

Gaston, K. 1996 Species-range-size distributions: patterns, mechanisms and implications. *Trends Ecol. Evol.* **11**, 197–201.

Glazier, D. S. 1980 Ecological shifts and the evolution of geographically restricted species of North American *Peromyscus* (mice). *J. Biogeog.* **7**, 63–83.

Gregory, R. D., Keymer, A. E. & Harvey, P. H. 1991 Life history, ecology, and parasite community structure in Soviet birds. *Biol. J. Linn. Soc.* **43**, 249–262.

Hammond, D. S. & Brown, V. K. 1995 Seed size of woody plants in relation to disturbance, dispersal, soil type in wet neotropical forest. *Ecology* **76**, 2544–2561.

Hansen, T. A. 1980 Influence of larval dispersal and geographic distribution on species longevity in neogastropods. *Paleobiology* **6**, 193–207.

Hanski, I. 1982 Dynamics of regional distribution: the core and satellite specise hypothesis. *Oikos* **38**, 201–221.

Harper, K. T. 1979 Some reproductive and life history characteristics of rare plants and implications of management. *Great Basin Naturalist Memoirs* **3**, 129–137.

Hartnett, D. C. & Bazzaz, F. A. 1983 Physiological integration among intraclonal ramets in *Solidago canadensis*. *Ecology* **64**, 779–788.

Hartnett, D. C. & Bazzaz, F. A. 1985 The integration of neighborhood effects by clonal genets of *Solidago canadensis* *J. Ecol.* **73**, 414–427.

Harvey, P. H. & Mace, G. M. 1982 Comparisons between taxa and adaptive trends: problems of methodology. In *Current problems in sociobiology* (ed. K. S. C. S. Group), pp. 343–361. Cambridge University Press.

Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford University Press.

Hodgson, J. G. 1986 Commonness and rarity in plants with special reference to the Sheffield flora. Part I: The identity, distribution and habitat characteristics of common and rare species. *Biol. Conservation* **36**, 199–252.

Hubbell, S. P. & Foster, R. B. 1986 Commonness and rarity in a Neotropical forest: implications for tropical tree conservation. In *Conservation biology: the science of scarcity and* *diversity* (ed. M. A. Soulé), pp. 205–231. Sunderland, MA: Sinuaer Associates.

Juliano, S. A. 1983 Body size, dispersal ability, and range size in North American species of Brachinus (Coleoptera: Carabidae). *Coleopterists Bull.* **37**, 232–238.

Karron, J. D. 1987 The pollination ecology of co-occurring geographically restricted and widespread species of Astragalus (Fabaceae). *Biol. Conservation* **39**, 179–193.

Kavanaugh, D. H. 1985 On wing atrophy in carabid beetles (Coleoptera: Carabidae), with special reference to Nearctic Nebria. *Taxonomy, phylogeny and zoogeography of beetles and ants* (ed. G. E. Ball), pp. 408–431. Dordrecht : Dr. W. Junk Publishers.

Kelly, C. K. 1994 On the economics of plant growth: stolon extension and resource acceptance in *Cuscuta europaea*. *Evol. Ecol.* **8**, 459–470.

Kelly, C. K. 1995*a* On clonal integration: facing the evolutionary context. *Evol. Ecol.* **9**, 575–585.

Kelly, C. K. 1995*b* Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia* 102, 377–388.

Kelly, C. K. 1996 Identifying plant functional types using floristic data bases: ecological correlates of plant range size. *J. Vegetation Sci.* **7**.

Kelly, C. K. & Beerling, D. J. 1995 Plant life form, stomatal density and taxonomic relatedness: a reanalysis of Salisbury (1927). *Funct. Ecol.* **9**, 422–431.

Kelly, C. K. & Purvis, A. 1993 Seed size and establishment conditions in tropical trees: on the use of taxonomic relatedness in determining ecological patterns. *Oecologia* **94**, 356–360.

Kelly, C. K. & Woodward, F. I. 1995 Ecological correlates of carbon isotope composition: A comparative analysis testing for the effects of temperature, CO_2 and O_2 partial pressure and taxonomic relatedness on $\delta^{13}C$ *J. Ecol.* **83**, 509–515.

King, D. A. 1991 The adaptive significance of tree height. *Am. Nat.* **135**, 809–828.

Krebs, C. J. 1994 *Ecology*, 4th edn. New York: Harper Collins.

Lawton, J. H. 1990 Species richness and population dynamics of animal assemblages. Patterns in body size, abundance, space. *Phil. Trans. R. Soc. Lond.* B **330**, 283–291.

Lawton, J. H. & Woodroffe, G. L. 1991 Habitat and the distribution of water voles: why are there gaps in a species' range? *J. Anim. Ecol.* **58**, 1021–1034.

Letcher, A. J. & Harvey, P. H. 1994 Variation in geographical range size among mammals of the Palearctic. *Am. Nat.* **144**, 30–39.

Longton, R. E. 1992 Reproduction and rarity in British mosses. *Biol. Conservation* **59**, 89–98.

Martins, E. P. & Garland Jr., T. 1991 Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**, 534–557.

Maurer, B. A. 1991 Concluding remarks: birds, body size, and evolution. *Acta XX Congressus Internationalis Ornithologici*, 835–837.

McCoy, E. D. 1990 The distribution of insects along elevational gradients. *Oikos* **58**, 313–322.

Nickrent, D. L. & Soltis, D. E. 1995 A comparison of angiosperm phylogenies from nuclear18s rDNA and *rbc*L sequences. *Annls Missouri Botanical Gardens* **82**, 208–234.

Oakwood, M., Jurado, E., Leishman, M. & Westoby, M. 1993 Geographic ranges of plant species in relation to dispersal morphology, growth form, and diaspore weight. *J. Biogeog.* **20**, 563–572.

Obeso, J. R. 1992 Geographic distribution and community structure of bumblebees in the northern Iberian peninsula. *Oecologia* **89**, 244–252.

Pagel, M. D. 1992 A method for the analysis of comparative data. *J. Theor. Biol.* **156**, 431–442.

Pagel, M. P., May, R. M. & Collie, A. R. 1991 Ecological aspects of the geographic distribution and diversity of mammal species. *Am. Nat.* **137**, 791–815.

Perring, F. H. & Walters, S. M. (ed.) 1982 *Atlas of the British flora*. London, U. K.: Botanical Society of the British Isles.

Primack, R. B. & Miao, S. L. 1992 Dispersal can limit local plant distribution. *Conservation Biol.* **6**, 513–519.

Purvis, A. 1992 Comparative methods: theory and practice. D.Phil., University of Oxford.

Purvis, A., Gittleman, J. L. & Luh, H.-K. 1994 Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *J. Theor. Biol.* **167**, 293–300.

Purvis, A. & Rambaut, A. 1995 Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Computer Applic. Biosci.* **11**, 247–251.

Rabinowitz, D., Cairns, S. & Dillon, T. 1986 Seven forms of rarity and their frequency in flora of the British Isles. In *Conservation biology: the biology of scarcity and diversity* (ed. M. E. Soulé), pp. 182–204. Sunderland, MA: Sinauer Associates.

Read, A. F. & Nee, S. 1995 Inference from binary comparative data. *J. Theor. Biol.* **173**, 99–108.

Reveal, J. L. 1981 The concepts of rarity and population threats in plant communities. In *Rare plant conservation* (ed. L. E. Morse & M. S. Henefin), pp. 41–46. New York: New York Botanical Garden, Bronx.

Ridley, M. 1983 *The explanation of organic diversity: the comparative method and adaptations for mating*. Oxford University Press.

Rubin, J. A. 1987 Growth and refuge location in continuous, modular organisms: experimental and computer simulation studies. *Oecologia* **72**, 46–51.

Söderström, L. 1989 Regional distribution patterns of bryophyte species on spruce logs in northern Sweden. *The Bryologist* **92**, 349–355.

Sokal, R. R. & Rohlf, F. J. 1995 *Biometry*, 3rd edn. New York: W. H. Freeman.

Sutherland, W. J. & Stillman, R. A. 1988 The foraging tactics of plants. *Oikos* **52**, 239–244.

Thomas, C. D. & Mallorie, H. C. 1985 Rarity, species richness and conservation: butterflies of the Atlas mountains in Morocco. *Biol. Conservation* **33**, 95–117.

Thorne, R. F. 1992 Classification and geography of the flowering plants. *Bot. Rev.* **58**, 225–348.

Turland, N. J., Chilton, L. & Press, J. R. 1993 *Flora of the Cretan area: annotated checklist and atlas*. London: The Natural History Museum.

Tutin, T. G., Burges, N. A., Chater, A. O. *et al.* (ed.) 1993 *Flora Europaea*. Cambridge University Press.

Van Valen, L. 1973 Body size and numbers of plants and animals. *Evolution* **27**, 27–35.

Wheelright, N. T. & Orians, G. H. 1982 Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* **119**, 402–413.

Woodward, F. I. & Kelly, C. K. 1995 The influence of CO_2 concentration on stomatal density. *New Phytol.* **131**, 311–327.

Discussion

M. J. CRAWLEY (*Department of Biology, Imperial College, Silwood Park, Ascot SL5 7PY*) I think your category of 'herbs' is too coarse, and hides important differences in the extent of distribution. You found no difference between trees and herbs, and yet *within* the herbs, hemicryptophytes have the largest average distributions and annuals and geophytes have the smallest. Trees are intermediate, so there is no difference between trees and the larger category of herbs (= hemicryptophytes + annuals + geophytes).

C. K. KELLY. Yes, the results from breaking down the 'woodies' category into trees and shrubs shows the value of further fine tuning the questions being asked. It will be interesting to see if the cross-species results that you have pointed out remain after phylogenetic relatedness is taken into account.