

A phylogenetic approach to community assembly from a local species pool

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Ecological theory provides two contrasting predictions about the characteristics of the species combining to form communities. Classical competition theory states that they will be less similar than expected by chance, whilst the environmental structuring hypothesis states that they will be more similar. We investigated these predictions by applying phylogenetic methods of analysis (PICs) to a grassland community, examining species on the basis of their traits. At the scale of investigation most useful in making predictions about the presence and abundance of species (the community level), the species forming the community were more similar than would be expected by chance. The use of PICs resulted in a more sensitive test than if phylogeny had been ignored, allowing the detection of effects that would otherwise have been overlooked or underestimated. Selected traits from the PICs analysis were used to develop a predictive model of community membership using discriminant analysis. This correctly identified species in the pool which were present in the community but failed to predict absences accurately, implying that dispersal limitation may operate in the community.

Keywords: plant; community assembly; traits; phylogeny; phylogenetically independent contrasts; dispersal limitation

1. INTRODUCTION

Ecologists have long been convinced that communities of organisms are not just random collections of species (e.g. Raunkiaer 1934; Williams 1947) and for over two decades they have attempted to model the way in which the actual community arises from the welter of possible species combinations (Diamond 1975). There are two contrasting ecological traditions regarding the types of non-randomness which may be observed in community assembly from a set of potential colonists. The first asserts that competition is of fundamental importance in shaping community composition and, in its classical form, states that competition is greatest between those species which are most similar (e.g. Darwin 1902, pp. 93–96). This was investigated and found to be the case by Johansson & Keddy (1991). The corresponding prediction is that the most stable (and, therefore, the most likely to be observed) community arises when coexisting species are dissimilar and traits are overdispersed with respect to an appropriate null hypothesis. In several cases where this hypothesis has been examined, statistically significant effects tending to support the theory have been observed (e.g. Armbruster *et al.* 1994; Wilson & Watkins 1994; Wilson & Gitay 1995) although such effects have at times proved elusive (e.g. Wilson *et al.* 1996).

However, there is an equally long-standing tradition in ecology and phytogeography (e.g. Schimper 1903; Raunkiaer 1934) which regards the species forming communities as being more similar to one another than would be expected by chance. Under a given set of environmental conditions, only those species possessing a limited set (or sets) of attributes will be able to establish themselves in the community (e.g. Montalvo *et al.* 1991) and traits

should appear underdispersed with respect to a null model. Underdispersion might be particularly observed in traits involved in overcoming environmental adversity (Weiher & Keddy 1995). These two schools of thought lead to quite opposite predictions about the sorts of species which comprise communities, but attempts to investigate community structure by means of species' characteristics almost invariably make reference to only one or other approach (although see Cody (1991) for a noteworthy exception). Previous studies of this problem have also treated species as independent data points and, thus, were prone to pseudoreplication (Harvey & Pagel 1991). It is particularly important not to treat each species as an independent data point when analysing the relationship between traits and community assembly. Analyses of species:genus ratios typically show that communities contain more species per genus than expected (Williams 1947), implying that the ecological similarities found among related species play a role in community assembly.

In this paper we use phylogenetically independent contrasts (PICs), a method designed to avoid pseudoreplication, to compare the species in a community with those in the local species pool and to determine how ten ecological traits correlate with community membership. We then test how well the traits identified as significant in the PIC analysis are able to predict the presence and observed abundance (Poff 1997) of species found in the community.

2. METHODS

(a) *The field site and study community*

Our study community was a 4-ha area of grassland typical of lowland England at Little Wittenham, Oxfordshire (grid reference SU 568 924) which has been the subject of detailed ecological studies for more than a decade (e.g. Silvertown & Smith 1989; Treweek 1990; Silvertown *et al.* 1992; Bullock *et al.* 1994; Watt *et al.* 1996; Treweek *et al.* 1997). The site was grazed by sheep and had basic (*ca.* pH 7.5), relatively deep, well-drained

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Table 1. *Definitions of traits and variables used in the analysis*

trait	variable	definition and range of values	source of data
competitive ability	COMP	score based on Grime's CSR classification: C = 12, CR = 6 and CSR = 4	Grime <i>et al.</i> (1988)
nutrient level	NUTR	1–8, low to high	Ellenberg <i>et al.</i> (1991)
flowering period	TOTFLO	flowering period (months)	Clapham <i>et al.</i> (1987)
	FLO	flowering period outside the summer grazing period June–October (months)	Clapham <i>et al.</i> (1987)
plant height	MINHT	lower bound of height range (cm)	Clapham <i>et al.</i> (1987) and Stace (1991)
	MAX HT	upper bound of height range (cm)	Clapham <i>et al.</i> (1987) and Stace (1991)
dispersal	DISP	good or poor	Grime <i>et al.</i> (1988)
seed weight	SDWT	mean value (mg)	Grime <i>et al.</i> (1988)
vegetative reproduction	VEG	present or absent	Grime <i>et al.</i> (1988)
longevity	ANN	annual or perennial	Clapham <i>et al.</i> (1987)
	LONGV score	annuals = 1, biennials = 2, pauciennials = 3 and perennials = 5	Clapham <i>et al.</i> (1987)
abundance	ABUND	number of 10 km squares occupied within a 110 km × 110 km square centred on the field site	Perring & Walters (1962)
seed bank	SDBNK	present or absent	Hodgson <i>et al.</i> (1995)

and fertile soils. A list of 36 naturally occurring species at the site was drawn up from systematic surveys over a three-year period. The abundance of each species in the local species pool was quantified as the frequency of 2 m × 2 m quadrats occupied out of a sample of 80. The study reported here examines broad-leaved species only, because they comprise a diverse set of species which is particularly amenable to study.

(b) *The local species pool*

We defined the local species pool from the intersection of two sets of species: the set listed in the National Vegetation Classification (NVC) (Rodwell 1992) as occurring in grassland communities on non-acid, non-waterlogged soils (NVC types MG1, MG5, MG6, MG7, CG3, CG4, CG5 and CG6) and the set of species which had been recorded (Perring & Walters 1962) as present within a 50 km × 50 km square centred on the field site. All aspects of the environment (e.g. soil depth) at the study site mentioned in the NVC community descriptions were taken into account except for details of management regime, since the effects of management are investigated as part of this study. The circumscription of the species pool is discussed more fully in Tofts (1998). Two species of lowland mesotrophic and calcareous grasslands which were absent from the NVC lists because of their rarity were identified by reference to the habitat descriptions in Clapham *et al.* (1987) and added to the species pool. The species pool is listed in Appendix A. The plant names follow Kent (1992, 1996).

(c) *Traits*

Values for ten ecological traits likely to affect community assembly were obtained for the species pool from published sources (table 1). Seven traits were measured by one variable each and three traits were measured by two variables each, making 13 variables in all. Since the data were taken from a number of different sources there were some missing values. Depending upon the variable, the data were either binary or continuous (ordinal data were treated as continuous). We hypothesized devia-

tions in trait values between the species pool and the local community as follows (variable names are given in parentheses).

Due to the agricultural history of the site, perennial species (ANN and LONGV) with high competitive ability (COMP), high nutrient values (NUTR) and vegetative reproduction (VEG) should be overrepresented. Assuming that recruitment from seed is important, species with a longer flowering period (TOTFLO) or which flower for a greater length of time outside the summer grazing period (FLO) should be favoured and greater seed weight (SDWT) should be advantageous. Grazing should favour shorter species (MINHT and MAXHT) and better dispersers (DISP) should be overrepresented. We had no prior expectation of how the existence of a seed bank (SDBNK) would affect community membership. Higher local abundance (ABUND) was expected to increase the likelihood of community membership.

(d) *Phylogeny*

A phylogeny is required in order to apply PICs. No complete phylogenetic tree which resolves the relationships between the taxa in our species pool right down to the species level exists. We therefore constructed a super-tree (Sanderson *et al.* 1998) by combining phylogenetic information from multiple sources, as listed in Appendix B (a copy of the super-tree is available from the authors on request).

(e) *Data analysis*

Binary variables were analysed by the PIC method of Read & Nee (1995) using the sign test. PICs for continuous variables were obtained using the method of Felsenstein (1985), as implemented by the CAIC computer package (Purvis & Rambaut 1995) with the branch lengths set equal. Ordinal data were treated as continuous because no PIC method applicable to ordinal data exists. Due to this departure from standard statistical assumptions of the method and because the local species pool comprised an entire statistical population rather than a random sample, we used a randomization test to evaluate the statistical significance of the results (Manly 1991). Depending upon the trait in question, the data set contained between

Table 2. Results of the analysis of trait values and trait dispersion

(n is the number of PICs used in the analysis of the trait values. The directions of significant differences in the mean trait values for contrasts between species present (p) and absent (a) from the local community are shown by an inequality. For the variance ratio the null value is 1, with overdispersion resulting in a larger ratio and underdispersion resulting in a smaller one. The p -values are two-tailed. One-tailed values are approximately half the probabilities shown. The Bonferroni-corrected 5% cut-off is at $p = 0.0051$.)

variable	n	mean trait values based on PICs		dispersion based on trait value of species	
		present versus absent	p	variance ratio	p
COMP	33	p > a	0.0008	2.041	0.1530
NUTR	34	p > a	0.0053	0.555	0.0275
TOTFLO	23	p > a	0.0012	0.473	0.4436
FLO	23	p > a	0.0173	0.700	0.7184
MINHT	37	—	0.7091	0.694	0.3929
MAXHT	37	—	0.4619	0.950	0.8952
DISP	15	—	0.1186	0.863	0.0945
SDWT	32	—	0.6304	0.866	0.4979
VEG	27	—	0.2476	1.2000	0.0673
ANN	12	—	0.2268	1.4030	0.4153
LONGV	37	—	0.9795	1.1330	0.6867
ABUND	35	p > a	<0.0001	0.1050	<0.0001
SDBNK	33	—	0.9463	0.7892	0.3438

12 and 37 contrasts (see table 2). The randomization tests took the following form. Two mutually exclusive groups of species (i.e. sampling without replacement) were drawn at random from the full data set, with the number of species in each group being equal to the number of contrasts for the trait under investigation. A t -test was performed on the two randomly selected groups and the value of the t -statistic recorded. This process was repeated 10 000 times and the statistical significance of the actual t -value assessed against the randomizations.

The under- and overdispersions of traits were investigated using randomization tests. The variance for a particular trait was calculated for the s species within the study community ($\text{var}_{\text{within}}$) for which there were trait data and then the variance for an equal number of species randomly chosen from the species pool but not occurring in the study community ($\text{var}_{\text{outside}}$) was calculated. The $\text{var}_{\text{within}}:\text{var}_{\text{outside}}$ ratio indicates whether traits are over- or underdispersed in comparison with the expected value of 1. Statistical significance was determined by randomly selecting two mutually exclusive groups of s species from the entire species pool, calculating the variance ratio and repeating the process 10 000 times. The observed variance ratio was then compared against the null distribution to assess the statistical significance.

Discriminant analysis with cross-validation was performed using the linear discriminant function (Fisher 1936; Krzanowski 1988) to predict the presence and abundance of species in the local community (measured by frequency in 80 quadrats) from the values of the traits that PIC analysis showed to be statistically significant. Prior probabilities, although known, were not used because the omission makes a more stringent and realistic test. Spearman's rank correlation was used to compare the probability of species occurrence generated by the discriminant function and observed abundance in the community.

3. RESULTS

Significant differences in the mean trait values were found for the variables COMP, NUTR, TOTFLO, FLO

and ABUND, all of which were in the expected direction (table 1). Significant underdispersion was identified for ABUND and, marginally, for NUTR (table 2). Two-tailed tests were used to test the significance of trait dispersion because of the conflicting predictions of ecological theory.

Of the five statistically significant traits identified, ABUND gave the best model as a predictor of local community membership in discriminant analysis. Addition of TOTFLO to the model containing ABUND improved the predictions of the discriminant analysis, though this improvement was not statistically significant ($p > 0.05$). The classification scores were calculated as $S_0 = -5.60202 + 0.07585(\text{ABUND}) + 1.04542(\text{TOTFLO})$ and $S_1 = -9.66530 + 0.11067(\text{ABUND}) + 1.20743(\text{TOTFLO})$, where S_0 denotes the score for membership of the group predicted to be absent from the local community and S_1 denotes the score for membership of the group of species predicted to be present. A species was placed in the group for which it had the highest score, producing the following results: 33 out of 34 (97%) species actually present in the study community were correctly predicted to be present and 70 out of 115 (61%) species actually absent from the community were correctly classified as absent. Overall, the proportion of correctly classified species was 69%. The errors in assignment to groups were highly unbalanced with actual members of the study community being predicted well, but with 45 out of 115 actual absentees being predicted to be present.

There was a highly significant statistical relationship between the predicted likelihood of occurrence in the local community and the abundance of the species in it ($r_s = 0.495$, $n = 149$ and $p \ll 0.0001$). In particular, species with a low estimated probability of occurrence were indeed either rare or absent from the community (figure 1 and Appendix A); all except the rarest species in the community had a discriminant probability of 0.65 or more.

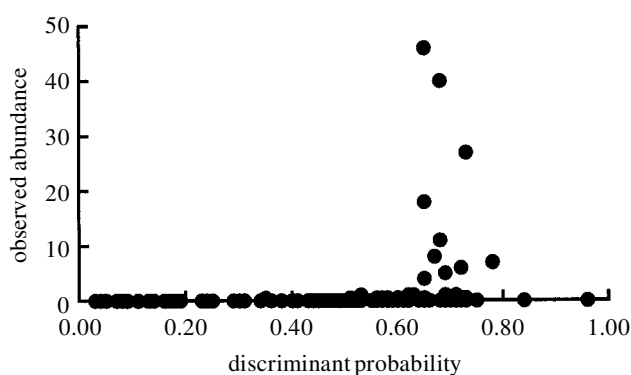


Figure 1. Probability of broad-leaved species being present in the community, as modelled using discriminant function, plotted against the actual abundance of these species in the community.

4. DISCUSSION

Four traits were implicated a role in the assembly of the study community by significant differences between the species that were present and relatives in the local pool that were absent. Flowering (TOTFLO and FLO), abundance in the surrounding landscape (ABUND), competitive ability (COMP) and nutrient requirement (NUTR) all differed in the expected direction. Thus, there is support for the hypothesis that species with restricted flowering times are prevented from recruiting into the community by grazing and for the hypotheses that weak competitors (*sensu* Grime 1979) and species with low nutrient requirements are excluded from the community by interspecific competition. The practical value of using PICs rather than comparisons between species without correction for phylogenetic relationships has been questioned (Ricklefs & Starck 1996), so we repeated the tests ignoring phylogeny. Doing this (R. Tofts and J. Silvertown, unpublished data) we found insignificant differences ($p > 0.1$) in competitive ability (COMP) in strong contrast to the test described here, despite the greater degrees of freedom in pseudoreplicated tests. The effect of FLO was also missed and TOTFLO was judged to be much less significant. In both cases, the effect of ABUND was judged to be highly significant and only in the case of NUTR did the spuriously high degrees of freedom yield a slightly more significant result. Thus, the use of PICs in this case has resulted in a more sensitive test, allowing the detection of ecological patterns which otherwise would have been overlooked or underestimated.

Significant or marginally significant underdispersion was detected for two variables (NUTR and ABUND). Underdispersion is a by-product of the fact that trait values in one section of the scale (e.g. species with a high nutrient requirement) are favoured. With the exception of competitive ability (COMP), the other traits which showed significant differences in their mean values were also underdispersed although not significantly so. No convincing evidence of overdispersion was found for any trait investigated.

The discriminant function worked well in assigning species present in the community to their correct group, but it performed poorly in assigning absent species to the correct group. This imbalance in allocation is of interest

because, although it may reflect the use of an unrealistically simple model (linear discriminant function) or inadequate predictors, we know that the species richness of the local community has been increasing slowly over the ten years during which it has been monitored (Watt *et al.* 1996). It may be the case that some of the species erroneously predicted to be present would now be able to inhabit the site but have not yet colonized it due to dispersal limitation. This possibility has been investigated experimentally and receives some support in a study which will be reported elsewhere.

Do the findings reported in this paper favour the competitive or the environmental structuring hypothesis? Several significant relationships between traits and presence in the study community were found and, in all statistically significant cases, trait underdispersion associated with the differences in trait value was recorded. Our results therefore support the environmental structuring hypothesis. This does not mean that competition is unimportant as a structuring force in plant community assembly (Silvertown *et al.* 1999), but its effects are most likely to be seen at the scale over which plants interact with one another, which is a much smaller scale than that at which ecologists would normally wish to make predictions about vegetation.

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APPENDIX A: THE LOCAL SPECIES POOL

Table A1. *The local species pool (eudicots only) and the predicted probability of occurrence (p) in the community from the model described in the text*

(Species marked in bold type were present in the community.)

species	p
<i>Achillea millefolium</i>	0.65
<i>Aegopodium podagraria</i>	0.62
<i>Agrimonia eupatoria</i>	0.62
<i>Allium vineale</i> ^a	
<i>Anacamptis pyramidalis</i>	0.14
<i>Anthriscus sylvestris</i>	0.65
<i>Anthyllis vulneraria</i>	0.25
<i>Arctium minus</i>	0.66
<i>Artemisia vulgaris</i>	0.56
<i>Asperula cynanchica</i>	0.14
<i>Astragalus danicus</i>	0.03
<i>Bellis perennis</i>	0.78
<i>Blackstonia perfoliata</i>	0.14
<i>Campanula glomerata</i>	0.23
<i>Campanula rotundifolia</i>	0.43
<i>Capsella bursa-pastoris</i>	0.96
<i>Carduus nutans</i>	0.40
<i>Carlina vulgaris</i>	0.25
<i>Centaurea nigra</i>	0.69
<i>Centaurea scabiosa</i>	0.58
<i>Centaureum erythraea</i>	0.46
<i>Cerastium fontanum</i>	0.73

Continued

Table A1. (Cont.)

species	p	species	p
<i>Cerastium glomeratum</i>	0.57	<i>Papaver dubium</i>	0.48
<i>Chaerophyllum temulentum</i>	0.49	<i>Papaver rhoeas</i>	0.70
<i>Chamerion angustifolium</i>	0.64	<i>Pastinaca sativa</i>	0.57
<i>Cirsium acaule</i>	0.47	<i>Picris hieracioides</i>	0.14
<i>Cirsium arvense</i>	0.65	<i>Pilosella officinarum</i>	0.55
<i>Cirsium eriophorum</i>	0.16	<i>Pimpinella major</i>	0.04
<i>Cirsium vulgare</i>	0.68	<i>Pimpinella saxifraga</i>	0.49
<i>Clinopodium vulgare</i>	0.44	<i>Plantago lanceolata</i>	0.72
<i>Coeloglossum viride</i>	0.07	<i>Plantago major</i>	0.73
<i>Colchicum autumnale</i>	0.08	<i>Plantago media</i>	0.65
<i>Conopodium majus</i>	0.45	<i>Polygala calcarea</i>	0.08
<i>Convolvulus arvensis</i>	0.69	<i>Polygala vulgaris</i>	0.36
<i>Crepis biennis</i>	0.05	<i>Potentilla erecta</i>	0.52
<i>Crepis capillaris</i>	0.63	<i>Potentilla anserina</i>	0.66
<i>Crepis vesicaria</i>	0.51	<i>Potentilla reptans</i>	0.69
<i>Cruciata leavipes</i>	0.23	<i>Primula veris</i>	0.58
<i>Cynoglossum officinale</i>	0.51	<i>Prunella vulgaris</i>	0.69
<i>Dactylorhiza fuchsii</i>	0.04	<i>Pulsatilla vulgaris</i>	0.03
<i>Daucus carota</i>	0.60	<i>Ranunculus acris</i>	0.63
<i>Erigeron acer</i>	0.13	<i>Ranunculus bulbosus</i>	0.53
<i>Euphrasia officinalis</i>	0.36	<i>Ranunculus ficaria</i>	0.56
<i>Filipendula vulgaris</i>	0.16	<i>Ranunculus repens</i>	0.69
<i>Fragaria vesca</i>	0.66	<i>Reseda lutea</i>	0.34
<i>Galium aparine</i>	0.65	<i>Reseda luteola</i>	0.31
<i>Galium mollugo</i>	0.60	<i>Rhinanthus minor</i>	0.43
<i>Galium pumilum</i>	0.04	<i>Rumex acetosa</i>	0.62
<i>Galium verum</i>	0.61	<i>Rumex conglomeratus</i>	0.30
<i>Gentianella amarella</i>	0.19	<i>Rumex crispus</i>	0.69
<i>Gentianella germanica</i>	0.04	<i>Rumex obtusifolius</i>	0.71
<i>Geranium columbinum</i>	0.11	<i>Rumex sanguineus</i>	0.52
<i>Geranium dissectum</i>	0.67	<i>Salvia horminoides</i>	0.05
<i>Geranium molle</i>	0.72	<i>Sanguisorba minor</i>	0.53
<i>Geranium pratense</i>	0.45	<i>Saxifraga granulata</i>	0.14
<i>Glechoma hederacea</i>	0.65	<i>Scabiosa columbaria</i>	0.24
<i>Gymnadenia conopsea</i>	0.13	<i>Senecio erucifolius</i>	0.41
<i>Helianthemum nummularium</i>	0.38	<i>Senecio jacobaea</i>	0.69
<i>Heracleum sphondylium</i>	0.69	<i>Serratula tinctoria</i>	0.13
<i>Hippocrepis comosa</i>	0.16	<i>Silaum silaus</i>	0.16
<i>Hypericum perforatum</i>	0.65	<i>Sonchus asper</i>	0.59
<i>Hypochaeris radicata</i>	0.58	<i>Stachys officinalis</i>	0.40
<i>Iberis amara</i>	0.04	<i>Stellaria graminea</i>	0.53
<i>Inula conyza</i>	0.16	<i>Stellaria media</i>	0.96
<i>Knautia arvensis</i>	0.57	<i>Succisa pratensis</i>	0.53
<i>Lamium album</i>	0.84	<i>Taraxacum officinale</i>	0.65
<i>Lathyrus pratensis</i>	0.68	<i>Teucrium scorodonia</i>	0.17
<i>Leontodon autumnalis</i>	0.60	<i>Thesium humifusum</i>	0.05
<i>Leontodon hispidus</i>	0.65	<i>Thymus polytrichus</i>	0.34
<i>Leontodon taraxacoides</i>	0.35	<i>Thymus pulgioides</i>	0.09
<i>Lepidium campestre</i>	0.11	<i>Torilis japonica</i>	0.48
<i>Leucanthemum vulgare</i>	0.66	<i>Tragopogon pratensis</i>	0.56
<i>Linaria vulgaris</i>	0.57	<i>Trifolium campestre</i>	0.48
<i>Linum catharticum</i>	0.50	<i>Trifolium dubium</i>	0.75
<i>Listera ovata</i>	0.50	<i>Trifolium medium</i>	0.17
<i>Lotus corniculatus</i>	0.69	<i>Trifolium pratense</i>	0.72
<i>Malva moschata</i>	0.29	<i>Trifolium repens</i>	0.68
<i>Medicago lupulina</i>	0.71	<i>Urtica dioica</i>	0.65
<i>Onobrychis vicifolia</i>	0.30	<i>Veronica arvensis</i>	0.73
<i>Ononis repens</i>	0.40	<i>Veronica chamaedrys</i>	0.72
<i>Ononis spinosa</i>	0.18	<i>Veronica serpyllifolia</i>	0.70
<i>Ophioglossum vulgatum</i> ^a		<i>Vicia cracca</i>	0.59
<i>Ophrys apifera</i>	0.14	<i>Vicia hirsuta</i>	0.43
<i>Orchis morio</i>	0.13	<i>Vicia sativa</i>	0.59
<i>Orchis ustulata</i>	0.04	<i>Vicia sepium</i>	0.68
<i>Origanum vulgare</i>	0.25	<i>Vicia tetrasperma</i>	0.25
		<i>Viola hirta</i>	0.36

^a The probability was not calculated because one or more of the variables used in the model was not available for the species.

APPENDIX B: SOURCES OF THE PHYLOGENETIC DATA USED IN CONSTRUCTION OF THE SUPER-TREE

The relationships between families in the tree were taken from Chase *et al.* (1993). The within-family phylogenetic relationships were taken from the following sources: Jansen *et al.* (1990), Bremer (1994) and Susanna *et al.* (1995) for Asteraceae, Caputo & Cozzolino (1994) for Dipsacaceae, Chappill (1995) and Doyle (1995) for Fabaceae, Downie & Katz-Downie (1996) and Plunkett *et al.* (1996) for Apiaceae, Hsiao *et al.* (1995) and Pillay & Hilu (1995) for Poaceae, Plunkett *et al.* (1995) for Juncaceae and Cyperaceae and Wagstaff *et al.* (1995) for Lamiaceae. In the case of families where a phylogeny was unavailable, we used the taxonomic relationships according to Stace (1991) and Mabberley (1990) as a surrogate.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.