Phylogeny and the niche structure of meadow plant communities

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Summary

1 Because related species tend to be ecologically similar, it has long been recognized that the phylogenetic relationships between species in a community are likely to influence its structure. Previous investigations of the influence of phylogeny on community structure have generally shown that congeneric species are more frequent than would be expected if communities were randomly assembled. Because, under most theories of coexistence, stable coexistence requires ecological differences between species, the apparent excess of coexisting congeners suggests that trait differences important to coexistence must be recently evolved, arising near the tips of phylogenetic trees.
2 We test this hypothesis in two meadow plant communities for which we have good evidence of niche segregation along axes defined by hydrological conditions.
3 Niche overlaps were calculated and compared against null models for (i) all species in the community, (ii) species within genera, (iii) genera within families, (iv) families within the eudicots and monocots, and (v) eudicots and monocots.
4 Against expectation, we found that community structure was the cumulative result of niche separation arising at a range of phylogenetic levels and therefore that niche differences have been accumulated through the evolutionary history of species.

Key-words: Angiospermae, coexistence, eudicot, hydrology, meadows, monocot, niche overlap, phylogeny, plant community structure

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Introduction

It has long been recognized that a connection exists, or *should* exist, between the closeness of the phylogenetic relationships between species in a community and the strength of competitive interactions between them. Darwin (1859) wrote:

> As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera.

This idea lay behind many early studies (e.g. Jaccard 1922; Elton 1946; Moreau 1948) of species–genus ratios in various communities that were conducted in the expectation that low ratios would result from the competitive exclusion of some species by their congeners. However, Williams (1947) showed that when observed, species–genus ratios in several plant and insect communities were tested against an appropriate null model, they actually tended to be higher than expected. This implies that either competitive exclusion does not influence community composition, or the ecological traits affecting the similarity of habitat 'choice' between congeners evolve at the level of the genus and above, while the traits that determine the ability of congeners to coexist evolve nearer to the tips of the phylogenetic tree.

As far as plant communities are concerned, the first of these conclusions seems improbable given the overwhelming experimental evidence that interspecific competition between plants is virtually universal (Grime 1979; Aarssen & Epp 1990; Goldberg & Barton 1992; Gurevitch *et al*. 1992; Casper & Jackson 1997). There is much less evidence bearing upon the alternative conclusion, if only because the mechanisms that permit coexistence in most plant communities are poorly understood, and there are many plausible models, several of which may operate simultaneously (Tilman 1982; Janzen 1970; Tilman 1994; Hurtt & Pacala 1995; Pacala

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1997). However, even though the mechanisms permitting coexistence may differ between models, most current theories of coexistence depend upon the presence of some form of trait difference and do not permit the stable coexistence of identical species (Chesson 1991). Therefore, almost regardless of the precise mechanism of coexistence that may apply, the taxonomic composition of a community should depend, at least to some degree, upon where in the phylogeny of plants the crucial trait differences between species have evolved. Where differences in relevant traits have evolved entirely at deep levels in the phylogeny, for example, at the family level, competitive exclusion should limit the number of species belonging to that family that are able to coexist. Where relevant traits have evolved differences below the level of the genus, congeneric species should be able to coexist.

The difficulty with testing these ideas lies in identifying the correct traits to measure, or as Darwin (1859) put it:

> We can dimly see why the competition should be most severe between allied forms, which fill nearly the same place in the economy of nature; but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life.

Although this statement is no longer true for individual cases, it is true that no consensus has been reached about which traits in general confer competitive superiority upon a species (Goldberg 1997), and also that the origins of community structure remain obscure for most plant communities. However, it is clear that the relevant traits must be measured in the conditions of species' realized niches with interspecific competitors present.

Silvertown *et al.* (1999) recently demonstrated that a trade-off between two particular traits is responsible for the structure found in meadow plant communities. In this paper we take advantage of this finding to investigate the phylogenetic origin of the observed community structure. We do this by calculating the degree of niche overlap occurring within communities for taxa of different rank in the angiosperm phylogenetic tree. We predicted that niche overlap should increase from being below its expected value when assessed between species within genera, to being above its expected value when assessed for families within the monocot and eudicot clades.

Methods

FIELD SAMPLING AND QUANTIFICATION OF NICHE AXES

The species composition of two English meadow plant communities was sampled by estimating percentage abundance of all angiosperm plant species in randomly placed 1-m^2 quadrats. At Tadham Moor, Somerset, 844 quadrats were sampled in a 22-ha area of MG8 *Cynosurus cristatus–Caltha palustris* species-rich grassland (Rodwell 1992). At a second site approximately 80 km away in Cricklade, Wiltshire, we sampled an MG4 *Alopecurus pratensis–Sanguisorba officinalis* species-rich grassland with 641 quadrats placed in a 44-ha area.

There is strong experimental and observational evidence that these meadow plant communities are structured by interspecific competition along soil moisture gradients. Ellenberg (1953) grew six meadow grasses, including four species present in our communities and two with congeners in our communities, along an experimental water-table gradient in mixture and in monoculture. Silvertown *et al.* (1999) computed median pairwise niche overlaps using Pianka's (1973) index (α) for the six species in Ellenberg's mixture and monoculture treatments and found that while species distributions along the gradient (measured in terms of biomass) were highly overlapping ($\alpha = 0.94$) when grown in monoculture, median overlap was significantly ($P < 0.0001$) reduced by interspecific competition in the mixture ($\alpha = 0.72$).

In the field at Tadham and at Cricklade, we determined soil moisture conditions in each quadrat from its location in relation to surrounding water courses using hydrological models based on analytical solutions to drainage equations (Youngs *et al.* 1989; Gowing & Youngs 1997). A separate model was developed for the particular conditions at each of the sites. The hydraulic properties of the soil were directly measured *in situ* from a sample of five positions across each of the sites. At each of these positions, a 100-mm diameter auger hole was made and the single auger-hole method used (van Beers 1963). The estimates were then confirmed by taking a further three samples as undisturbed cores, each with a diameter of 150 mm, and assessing them in the laboratory using a falling-head permeameter (Klute & Dirksen 1986). The models were run as a series of *quasi* steady states on a weekly time-step. The input data consisted of measurements of the mean water levels in surrounding water courses, the incident rainfall and the evapotranspiration, as calculated from weather station data using the Penman–Monteith equation. The output from the models was in the form of weekly water-table elevations and was generated for a period of 15 years (1980–94) at each of the sites using historic records of water-course levels and meteorological data.

The duration of physiologically extreme conditions of aeration stress (caused by waterlogging) and soil drying occurring during the growing season (March through September) was quantified by calculating two sum exceedence values (Sieben 1965) for each quadrat. A sum exceedence value for soil drying (SEV$_d$) was cumulated during periods in which the soil moisture tension exceeded a level (0.5 m) that could potentially induce stomatal closure (Henson *et al.* 1989). SEV for aeration (SEV$_a$) was cumulated during periods in which the soil air-filled porosity fell below a level (10% by voulme) that precludes free diffusion of oxygen in the topsoil (Wesseling & van Wijk 1957). Both SEVs were

in units of metre weeks and had the advantage that they incorporate a measure of long-term (15-year) temporal variation in soil moisture at a scale relevant to the physiological tolerances of plants. High values of SEV_a indicated waterlogging and high values of SEV_d indicated drought.

The model predictions were validated using data from observation wells that were monitored weekly over a period of 7 years. These wells were located at a subset of quadrat positions (five at the Tadham site and six at Cricklade). The observed data were summarized by exactly the same method as for the model output to generate SEV_a and SEV_d. The modelled values were then plotted against the observed values. A regression line fitted through the origin gave $R^2 = 0.97$ for SEV_d and $R^2 = 0.99$ for SEV_a.

Using SEV_a and SEV_d as niche axes, we defined a two-dimensional niche space. For the purposes of computing niche overlap this space was divided into a grid of 'niche boxes' at each of two scales: 0.5×0.5 SEV units (fine scale) and 1×1 SEV units (coarse scale). Silvertown *et al.* (1999) demonstrated the existence of community structure by showing that median pairwise niche overlaps (α) between the most abundant species ($n = 64$ at Tadham, $n = 51$ at Cricklade) were significantly ($P < 0.0001$) less than random expectation at both scales at Tadham and at fine scale at Cricklade. Mean values of SEV_a and SEV_d were calculated for each species at each site, weighted by species' relative abundance in niche boxes. Highly significant trade-offs were demonstrated between the SEV axes when species were compared, indicating that this was the proximal cause of niche specialization under conditions of interspecific competition in the field.

DATA ANALYSIS

A taxonomic hierarchy was used as a surrogate for phylogenetic relationships, employing the species, genus and family definitions of Stace (1991), and membership of eudicot and monocot clades, as defined by the Angiosperm Phylogeny Group (Bremer *et al.* 1998). Though not ideal (see Discussion), this procedure is acceptable if the taxonomic groups used are monophyletic, as indeed appears to be the case. The taxonomic hierarchy is shown in Fig. 1.

For each of the two communities, and at both scales, we cumulated abundances in niche boxes into three nested levels of the taxonomic hierarchy: species were cumulated into abundances for genera, genera into abundances for families, and families into abundances for eudicot and monocot clades. This procedure has the advantage that between-species differences are averaged out before generic overlaps are compared, and so on up the taxonomic hierarchy. The mean value of Pianka's index of niche overlap (α) was computed for all pairwise combinations of taxa within each of five nested levels of the taxonomic hierarchy, giving a mean index between (i) all species in the community,

(ii) species within genera represented by at least two species in the community, (iii) genera within families represented by at least two genera, (iv) families within the eudicots and monocots, and (v) eudicots and monocots.

Mean abundances were standardized so that they summed to 100% for each taxon across all niche boxes before overlaps were measured. Mean overlaps were calculated using the EcoSim computer program version 1.11 (Gotelli & Entsminger 1997) and tested against a null model using the RA4 randomization algorithm, which shuffled the observed abundances of taxa among niche boxes, keeping the location of any zero values fixed. This is a conservative procedure that produces null communities that are more similar to the observed communities than those produced by alternative null models (Gotelli & Graves 1996). Each randomization was run 1000 times and the significance of observed mean overlaps was tested against the distribution of the 1000 means of the random communities.

Results

As previously reported (Silvertown *et al.* 1999), observed average pairwise niche overlaps across all species were significantly smaller in both communities than those of the randomized, null communities (Table 1a,b). This was the case for both fine-grain and coarse-grain niche boxes at Tadham, but only for fine-grain niche boxes at Cricklade. However, in the analysis as a whole, results from the fine- and coarse-grain randomization tests were similar at both sites (Table 1a,b) and so only fine-grain results will be mentioned below. All the results may be seen in Table 1.

Niche overlaps between congeneric species were significantly smaller than expected in 3/13 genera (*Potentilla*, *Agrostis*, *Alopecurus*) at Tadham and in 4/7 genera (*Agrostis*, *Bromus*, *Carex*, *Festuca*) at Cricklade. Congeneric species overlapped more than expected in 2/13 cases (*Cirsium*, *Trifolium*) at Tadham, but in no cases at Cricklade. Niche overlap between confamilial genera was significantly less than expected in 4/10 families (Caryophyllaceae, Polygonaceae, Rosaceae, Juncaceae) and significantly more than expected in 2/10 families (Cyperaceae, Poaceae) at Tadham. At Cricklade the numbers were, respectively, 2/5 (Apiaceae and Poaceae) and 1/5 (Fabaceae). Niche overlaps between families within clades did not differ from random expectation in either the monocots or the eudicots at Tadham, but were less than expected between monocot families at Cricklade. The monocots and eudicots as a whole overlapped with each other significantly less than expected at both Tadham and Cricklade. The relative numbers of cases of taxa that showed aggregation (overlap significantly more than expected), random overlap or segregation (overlap significantly less than expected) at the two sites are shown in Fig. 2. This shows that segregation did not arise exclusively, or even predominantly, between closely related taxa near the tips of the angiosperm phylogeny.
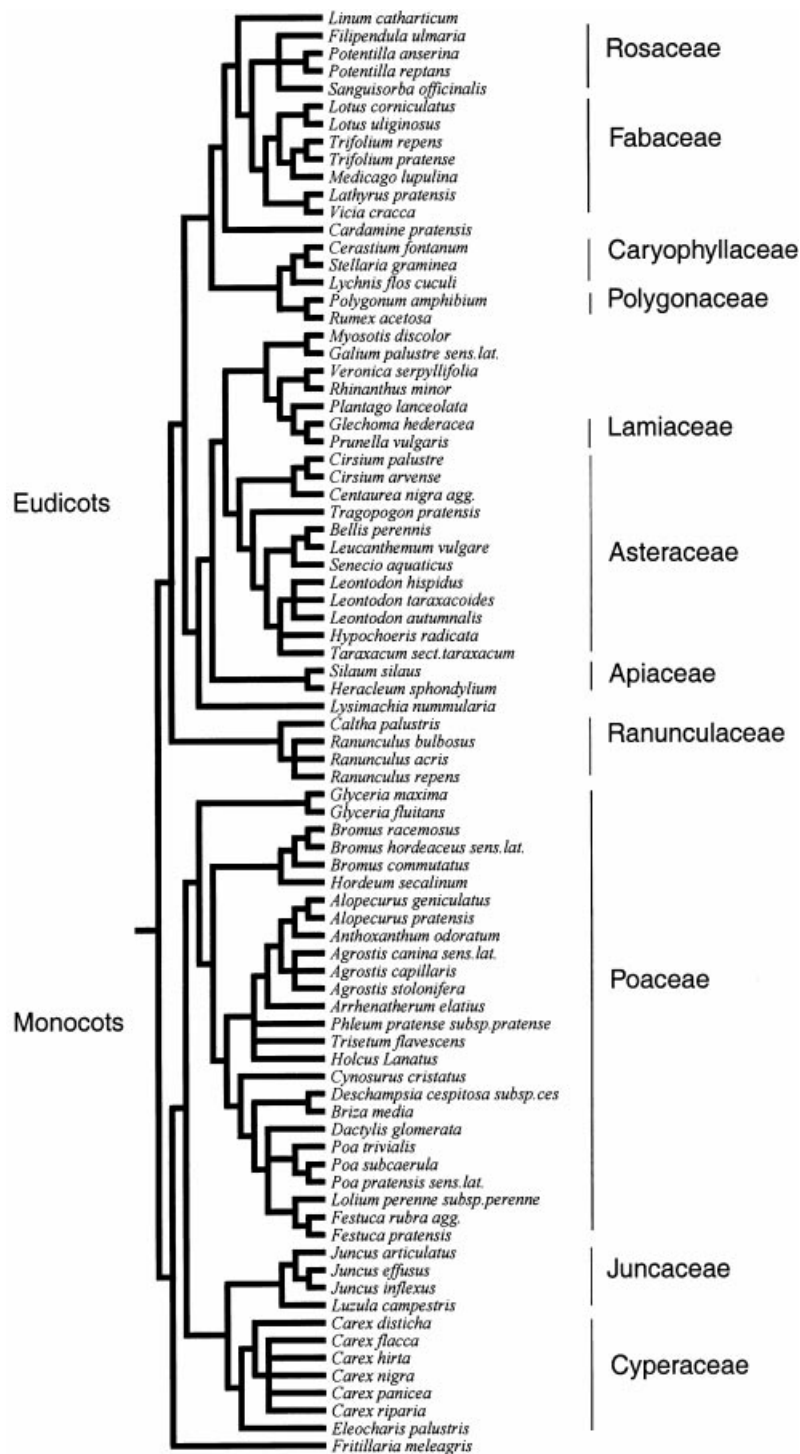
Fig. 1 A phylogenetic composite tree for the 82 species sampled in this study (some present at only one site), showing genus, family and clade membership. Note that this tree is more highly resolved than the taxonomic ranks that were actually used in our analyses. Sources of data are given in Appendix 1 in the *Journal of Ecology* archive on the World Wide Web (http://www.demon.co.uk/bes/journals).

Clade- and site-specific effects are also apparent from the results shown in Table 1. Eudicots behaved similarly at the two sites, showing aggregation of congeneric species as frequently as segregation, more frequent niche separation between confamilial genera, and no segregation between eudicot families. Monocots behaved differently at the two sites. At Cricklade, niche separation pervaded the entire monocot phylogeny occurring within *Carex* and within three grass genera, between grass genera, between monocot families, and between monocots and eudicots. Monocots at Tadham showed much weaker niche segregation: segregation occurred between congeneric species in only 2/8 genera, between the genera *Juncus* and *Luzula* in Juncaceae, but not between *Carex* and *Eleocharis* in Cyperaceae or between 13 genera in Poaceae, or between monocot families.

Table 1 Results of randomization tests for niche overlap at five taxonomic levels of analysis at two sites (Tadham and Cricklade). Number of tests in which observed overlaps were smaller than expected is shown. The number of times observed > expected = 1000 – (observed < expected). Sample size (*n*) for taxa above the species level are in units of the previous level

Taxonomic rank/taxa	Tadham			Cricklade		
	n	Fine-grain niches	Coarse-grain niches	*n*	Fine-grain niches	Coarse-grain niches
Species						
All species	64	1000***	1000***	51	999**	749
Genus						
Agrostis (M)	3	996**	522	2	1000***	1000***
Alopecurus (M)	2	999**	999**	–	–	–
Bromus (M)	2	444	421	2	974*	167
Carex (M)	6	299	77	2	955*	994**
Cirsium (E)	2	39†	9††	–	–	–
Festuca (M)	2	859	617	2	997**	985*
Glyceria (M)	2	143	117	–	–	–
Juncus (M)	3	736	463	–	–	–
Leontodon (E)	2	420	527	3	627	29†
Poa (M)	3	223	931	–	–	–
Potentilla (E)	2	975*	957*	–	–	–
Ranunculus (E)	2	813	135	3	908	673
Trifolium (E)	2	12†	1††	2	208	37†
Family						
Apiaceae (E)	–	–	–	2	1000***	994**
Asteraceae (E)	7	226	530	6	0†††	8†††
Caryophyllaceae (E)	3	953*	90	–	–	–
Cyperaceae (M)	2	6††	13†	–	–	–
Fabaceae (E)	3	909	896	5	39†	168
Juncaceae (M)	2	991**	989*	–	–	–
Lamiaceae (E)	2	205	170	–	–	–
Poaceae (M)	13	27†	1††	16	1000***	1000***
Polygonaceae (E)	2	1000***	1000***	–	–	–
Ranunculaceae (E)	2	919	893	–	–	–
Rosaceae (E)	2	1000***	990*	3	285	531
Clade						
Eudicots	13	883	57	12	234	58
Monocots	3	334	665	3	1000***	999***
Class						
Angiospermae	2	967*	478	2	1000***	909

For significant results in which observed overlap < expected, *P < 0.05, **P < 0.01, ***P < 0.001.
For significant results in which observed overlap > expected, †P < 0.05, ††P < 0.01, †††P < 0.001. (M), monocot species and families; (E), eudicot species and families.
– indicates no data because a taxon was rare, contained only one taxon of lower rank, or was absent.

Examples of various niche-overlap patterns between species are shown in Fig. 3, which shows the distribution of species' relative abundances plotted in hydrological niche space defined by SEV values. The three *Ranunculus* species appear to show segregation across niche space as a whole (Fig. 3a), but this was not significant in our tests (Table 1); *Heracleum sphondylium* and *Silaum silaus* are examples of confamilial species showing highly significant segregation (Fig. 3b). The three *Leontodon* spp. overlapped more than expected at the coarse scale at Cricklade (Fig. 3c), and two *Cirsium* spp. did so at both scales at Tadham (Fig. 3d).

Discussion

In both of the communities studied, meadow plant species segregated on hydrological (SEV) gradients, and this generated smaller-than-expected niche overlaps between species when an average overlap was computed for all pairwise combinations of species. This gross signature of community structure was the cumulative result of niche separation arising at a range of phylogenetic levels, namely species within genera (e.g. *Agrostis* spp.), genera within families (e.g. Apiaceae Fig. 3b), families within major clades, and between eudicot and monocot clades. The results were site-specific, showing that niche separation can arise at any and all phylogenetic levels. They were also clade-specific, showing, for example, a greater frequency and pervasiveness of niche separation in the monocots than in the eudicots at Cricklade. The pattern that we expected, with niche overlap within taxa increasing from lower to higher ranks, was not present. While it must be acknowledged that taxonomic ranks are artificial and may vary in

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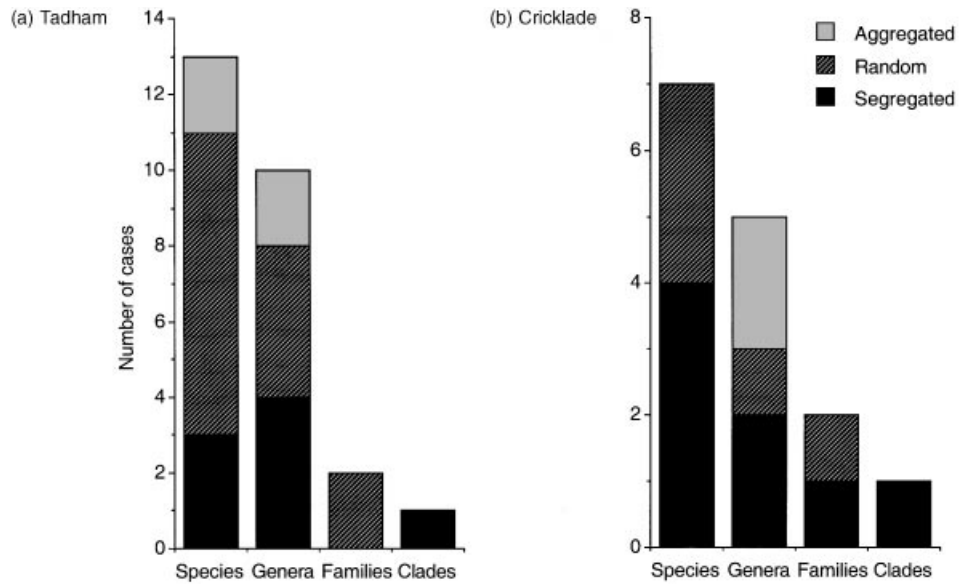
Fig. 2 Number of cases of niche overlap between taxa showing an aggregated, random or segregated pattern with respect to the expectations of null models. (a) Tadham, (b) Cricklade. Results are shown at the level of congeneric species, confamilial genera, families within monocot and eudicot clades and for overlap between the two clades themselves.
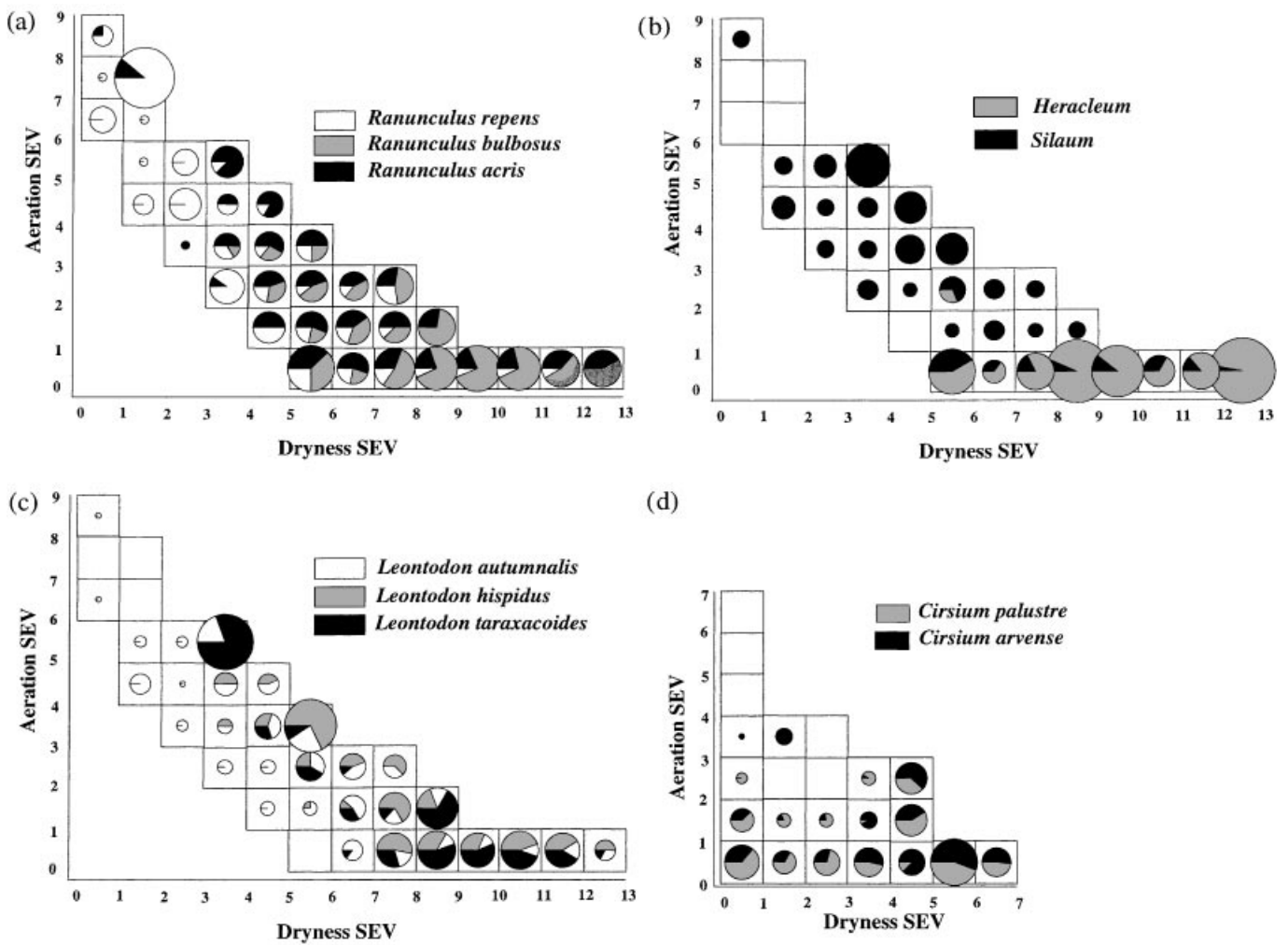
Fig. 3 Distribution of congeneric and confamilial species in a hydrologically defined niche space. The area of pies is proportional to the total abundance of species in different regions of the niche space. The niche boxes shown correspond to 1 SEV unit, which was the coarser-grain used in our analysis. (a) Ranunculus acris, R. bulbosus and R. repens at Cricklade. (b) Heracleum sphondylium and Silaum silaus (both Apiaceae) at Cricklade. (c) Leontodon hispidus, L. autumnalis and L. taraxacoides at Cricklade. (d) Cirsium palustre and C. arvense at Tadham.

meaning between groups, it seems reasonable to suppose that the niche segregation that we found between genera has a more recent evolutionary origin than that we found between families. This conclusion can be tested once we can measure the branch lengths on a proper phylogeny for the species in question (discussed later).

Some limitations of this analysis need to be considered. Our tests of niche segregation were conservative in two ways. First, our procedure for measuring and testing niche overlap treated each niche 'box' independently and ignored spatial autocorrelation of species distributions along gradients. Thus, visual inspection of the distribution of *Leontodon* spp. in niche space at Cricklade, for example (Fig. 3c), suggests that *L. hispidus* occurs in small amounts outside the niche space occupied by its two congeners, but this difference was not detected by our analysis (Table 1). In effect, our test disregarded larger-scale segregation and was sensitive to the finer-scale differences between species that are most appropriate when one is concerned with coexistence. The physical scale of quadrats (1 m2) placed an additional limit on the resolution possible in our test. Thus, we did not detect niche segregation in the distribution of *Ranunculus* (Fig. 3a, Table 1), a genus containing three meadow species that have been reported to segregate in relation to microtopography (Harper & Sagar 1953). Despite these scale limitations, overlaps at the two scales we examined were remarkably similar (Table 1), suggesting that our results were not over-sensitive to scale of measurement.

A second conservative feature of our procedure is that our null models of niche overlap assumed that species would be randomly distributed with respect to SEV gradients. However, the re-analysis of Ellenberg's (1953) experiment by Silvertown *et al*. (1999) showed that meadow species grown in monoculture along moisture gradients are not randomly distributed but overlap greatly. We do not know what the correct null distribution is for niches at our field sites, but Ellenberg's experiment strongly suggests that it is aggregated rather than random, implying Type II error (a tendency to accept a false null hypothesis) in our test of niche segregation. A similar problem may affect other niche studies.

When interpreting our results on the phylogenetic distribution of niche overlap, we must recognize that the species in our communities are but a rarefied sample of all the species that would be present in a complete phylogenetic tree of these groups. This does not compromise any of our conclusions concerning these individual communities, but it does mean that the results of such analyses will be sensitive to community composition. First, the value of niche overlaps will obviously depend upon the species present and their abundances. Second, and more subtly, because our field measurements relate to species' realized niches, the niche measurements themselves can be expected to vary depending upon which other species were present or dominant. Indeed, differences in our results between our two sites were, at least in part, due to floristic differences between Tadham and Cricklade. These

floristic differences may have been partly due to chance or management history, but they were also related to environmental differences between the sites that were not captured by our niche measurements. For example, Cricklade meadow has a more nutrient-rich mineral soil than Tadham, which probably explains the dominance of Poaceae over Cyperaceae at Cricklade.

We envisage two improvements to our method. First, the ideal approach to a phylogenetic analysis of community structure would be to use a true phylogeny rather than the taxonomic ranks we employed. Although we have constructed a composite tree from molecular phylogenies for the species in our communities (Fig. 1), we do not yet have a complete enough molecular data set to allow us to measure branch lengths in the tree, which would be essential to any analysis that ignored taxonomic rank. Second, more sophisticated null models could be constructed for expected niche overlap in the field. Although these would potentially reduce Type II error in the detection of niche segregation, choosing the right null model is notoriously difficult and making the wrong choice can easily lead to unacceptable Type I error rates (Gotelli & Graves 1996).

None of the caveats discussed above alter the two main conclusions of this study: (i) that niche segregation can result from an accumulation of trait differences through the evolutionary history of species, and (ii) that species can behave idiosyncratically, rendering taxon membership a poor guide to ecological behaviour. In general, plant community structure has proved elusive to detect and, so far as we know, this is the first study to dissect such structure in a phylogenetic manner. It is therefore an open question how typical our conclusions may turn out to be for plant communities as a whole.

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During the preparation of your manuscript for publication, the questions listed below have arisen. Please attend to these matters and return this form with your proof.

Many thanks for your assistance.

Quey Refs.	Query	Remarks
1	**Hurtt & Pacala 1997 has been changed to Hurtt & Pacala 1995 so this citation matches the list. Is this OK?**	
2	**Is Caryophyllaceae spelt correctly?**	
3	**Please provide state of: Burlington**	
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5	**Please provide journal title in full: Mèmoire Soc. Vaudoise Sci. Nat.,**	
6	**Please provide state of: Princeton**	
7	**Please complete page reference: pp.**	
8	**Please complete: Received ?????? 2000 revision accepted ?????? 2000**	