

air pipette system. The P4T-1 and P1T-2 dates are referenced to the Fish Canyon Sanidine monitor mineral using the published age of 28.02 Myr (ref. 27). The ages reported are arithmetic means of the individual dates based on total fusion analyses of single sanidine crystals. We report one standard deviation (s.d.) and standard error of the mean (s.e.) uncertainties with the mean ages to document crystal-to-crystal age variation. Individual crystal dates are presented in the Supplementary Information, Table 1.

In the incremental-heating experiment, 15 handpicked euhedral sanidine crystals were laid flat on the bottom of a 2-cm-diameter well of a copper sample disk. The crystals were heated by a CO<sub>2</sub> laser beam directed through an integrator lens that produces relatively even and uniform heating. Twenty-seven discrete temperature increments based on a controlled stepwise increase in power of the CO<sub>2</sub> laser were obtained. The heating time for each increment was 60 s. Incremental heating data are supplied in the Supplementary Information, Table 2.

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Supplementary information is available on Nature's World Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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## Hydrologically defined niches reveal a basis for species richness in plant communities

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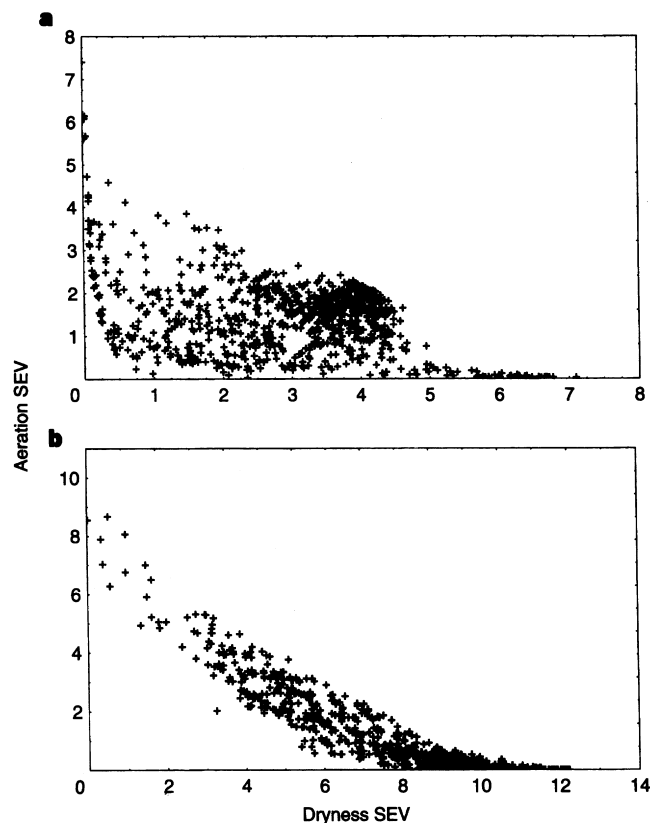
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Species-rich plant communities are prized repositories of biodiversity and a dwindling resource, but how the large numbers of species that characterize such communities are able to coexist is poorly understood. Resource-based competition theory predicts that stable coexistence between species depends on each being a superior competitor in its own niche<sup>1</sup>. The theoretical problem is that plants all require the same resources and acquire them in a very limited variety of ways, so observed niche overlaps are high<sup>2,3</sup> and exclusion of all but the best competitor is the predicted result. This problem, central to community ecology, has elicited a variety of theoretical solutions<sup>4–7</sup>, several of which invoke some degree of niche separation in time or space<sup>8,9</sup>. The signature of niche separation in the field is to be found in community structure, which should indicate (i) smaller than expected niche overlaps on relevant niche axes and (ii) a trade-off between species' resource use on orthogonal axes. Here we provide evidence for the existence of both these conditions in a species-rich plant community.

We sampled two English meadow plant communities (flood-plain meadows, NVC MG8 and MG4 (ref. 10)), at Tadham Moor, Somerset, UK, and at Cricklade, Wiltshire, UK. The percentage abundance of all species present was estimated in 844 1-m<sup>2</sup> quadrats within a 22-ha area at Tadham and in 641 quadrats within a 44-ha area at Cricklade. Species' tolerances were estimated from the range of hydrological conditions in which they were recorded growing in the field. Soil moisture conditions in each quadrat were determined from quadrat locations in relation to surrounding water courses by using two hydrological models parameterized with 15 years of data on meteorological inputs and weekly water levels in the surrounding rivers and ditches. The models were verified against water-table depths measured in dip-wells located at a subset of quadrat locations<sup>11,12</sup>. Two sum exceedence parameters<sup>13</sup> were derived from the modelled water-table depths and were used as niche axes. A sum exceedence value (SEV) for soil drying was cumulated during periods in which the moisture tension of the surface soil exceeded 5 kPa, which could potentially induce stomatal closure<sup>14</sup>. An SEV for aeration was cumulated during periods in which the soil air-filled porosity fell below 10% by volume, which is assumed to preclude the free diffusion of oxygen in the topsoil<sup>15</sup>. High aeration SEVs indicate waterlogging. The water-table depths that, under average summer evaporative demand, gave rise to (i) a surface tension of 5 kPa and (ii) an air-filled porosity of 10% were calculated for each of the soil types. These depths were then used as maximum and minimum thresholds, respectively. Each SEV gives the number of weeks for which the relevant threshold was exceeded multiplied by the vertical distance by which the water-table exceeded it, measured in units of metre weeks. SEVs have the advantage that they incorporate a measure of long-term temporal variation in soil moisture at a scale relevant to the physiological tolerances of plants.

Quadrat sampling locations were distributed randomly throughout the available niche space, as defined by the two SEV axes (Fig. 1). The Tadham site (Fig. 1a) is topographically very flat, whereas

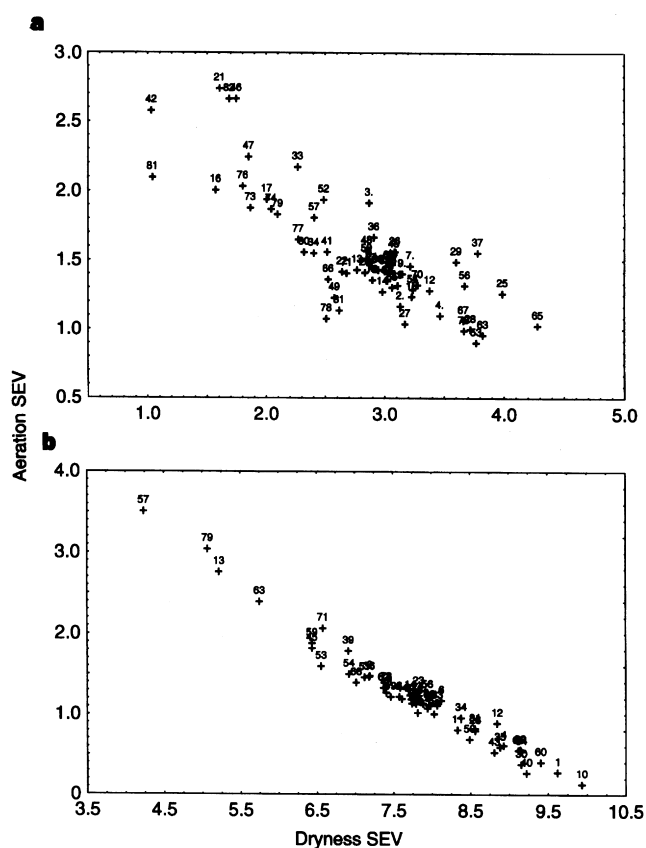


**Figure 1** Hydrologically defined niche space. Niche space at Tadham (a) and Cricklade (b). High aeration SEVs indicate frequently waterlogged conditions; high soil-dryness SEVs indicate frequently droughted conditions. Each point indicates a sampling location for plant community composition.

Cricklade has more variable microtopography resulting in a well-defined band of negatively correlated SEV parameters (Fig. 1b).

Pairwise values of Pianka's index of niche overlap<sup>16</sup> were computed for all combinations of species occurring in 50 or more quadrats (Tadham, 64 species; Cricklade, 51 species). Scale-dependence is to be expected in niche overlap, so indices were computed at two scales by dividing niche space at each site into 'boxes' of 0.5 SEV × 0.5 SEV (fine scale) and 1 SEV × 1 SEV (coarse scale). We calculated the mean abundance per box for each species, standardized to a total of 100% per species across all boxes. Departures of mean niche overlap for the whole community from random expectation were determined by using a randomization test<sup>17</sup> that randomized the non-zero abundances of species in boxes but kept zero abundances fixed. Mean pairwise niche overlaps were significantly less than expected ( $P < 0.0001$ ) at both fine and coarse scales at Tadham and at a fine scale at Cricklade. At the coarse scale, observed niche overlap at Cricklade was not significantly less than expectation ( $P = 0.25$ ). These results demonstrate that hydrologically defined niches structure both communities.

Experimental support for this conclusion comes from a reanalysis that we have performed of the results of a classic experiment by Ellenberg<sup>18</sup>. He sowed six meadow grass species, including four that occurred and two that had close relatives in our study, in single-species stands and in mixture evenly across an experimental water-table gradient spanning 5–140 cm mean water-table depth. SEVs for aeration and soil dryness on the gradient can be estimated; these span the entire range of values observed at Tadham and Cricklade. Dividing Ellenberg's hydrological gradient into ten 'niche boxes' and applying the same randomization test of niche overlap that we used on our own data, we find a degree of niche overlap (median 0.94) among species when grown in monoculture that is far higher than random expectation ( $P < 0.0001$ ). All species showed a peak in



**Figure 2** Trade-offs between dryness and aeration SEVs. Mean SEVs weighted by abundance for all species occurring in 50 or more quadrats at Tadham (a) and Cricklade (b). Key to species: 1, *Linum catharticum*; 2, *Filipendula ulmaria*; 3, *Potentilla anserina*; 4, *P. reptans*; 5, *Sanguisorba officinalis*; 6, *Lotus corniculatus*; 7, *L. uliginosus*; 8, *Trifolium repens*; 9, *T. pratense*; 10, *Medicago lupulina*; 11, *Lathyrus pratensis*; 12, *Vicia cracca*; 13, *Cardamine pratensis*; 14, *Cerastium fontanum*; 15, *Stellaria graminea*; 16, *Lychnis flos-cuculi*; 17, *Polygonum amphibium*; 18, *Rumex crispus*; 19, *R. acetosa*; 20, *Myosotis discolor*; 21, *Galium palustre sens. lat.*; 22, *Veronica serpyllifolia*; 23, *Rhinanthus minor*; 24, *Plantago lanceolata*; 25, *Glechoma hederacea*; 26, *Prunella vulgaris*; 27, *Cirsium palustre*; 28, *C. arvense*; 29, *Centaurea nigra* agg.; 30, *Tragopogon pratensis*; 31, *Bellis perennis*; 32, *Leucanthemum vulgare*; 33, *Senecio aquaticus*; 34, *Leontodon hispidus*; 35, *L. taraxacoides*; 36, *L. autumnalis*; 37, *Hypochoeris radicata*; 38, *Taraxacum* agg.; 39, *Silvaum silaus*; 40, *Heracleum sphondylium*; 41, *Lysimachia nummularia*; 42, *Caltha palustris*; 43, *Ranunculus bulbosus*; 44, *R. acris*; 45, *R. repens*; 46, *Glyceria maxima*; 47, *G. fluitans*; 48, *Bromus racemosus*; 49, *B. hordeaceus sens. lat.*; 50, *B. commutatus*; 51, *Hordeum secalinum*; 52, *Alopecurus geniculatus*; 53, *A. pratensis*; 54, *Anthoxanthum odoratum*; 55, *Agrostis canina sens. lat.*; 56, *A. capillaris*; 57, *A. stolonifera*; 58, *Arrhenatherum elatius*; 59, *Phleum pratense* subsp. *pratense*; 60, *Trisetum flavescens*; 61, *Holcus lanatus*; 62, *Cynosurus cristatus*; 63, *Deschampsia cespitosa* subsp. *cespitosa*; 64, *Briza media*; 65, *Dactylis glomerata*; 66, *Poa trivialis*; 67, *P. subcaerulea*; 68, *P. pratensis sens. lat.*; 69, *Lolium perenne* subsp. *perenne*; 70, *Festuca rubra* agg.; 71, *F. pratensis*; 72, *Juncus articulatus*; 73, *J. effusus*; 74, *J. inflexus*; 75, *Luzula campestris*; 76, *Carex disticha*; 77, *C. flacca*; 78, *C. hirta*; 79, *C. nigra*; 80, *C. panicea*; 81, *C. riparia*; 82, *Eleocharis palustris*; 83, *Fritillaria meleagris*.

biomass production in monoculture at between 20 and 35 cm design water-table depth. In contrast, niche overlap among the same species when in competition with one another (as in the field) was significantly reduced ( $P < 0.0001$ ; median overlap 0.72); species segregated along the water-table gradient, showing peaks in biomass over a wider range of 5–110 cm depending on species. This reanalysis not only demonstrates that our field observations can be reproduced experimentally, but also indicates that the null model of random niche overlap that we have used to detect the community

structure generated by hydrological conditions is very conservative because plants grown in the absence of interspecific competition have highly overlapping rather than randomly overlapping fundamental niches.

We used our field data to test for a trade-off between SEV axes. A mean SEV for each species on each axis at each site was calculated as  $(\sum_{i=1}^n SEV_i p_i) / n$ , where  $n$  was the number of quadrats in which a species was present,  $SEV_i$  was the value at the location of quadrat  $i$ , and  $p_i$  was the proportion of the species' total recorded abundance found in quadrat  $i$ . The distribution of mean SEV values in niche space (Fig. 2) shows a highly significant negative correlation between soil drying and waterlogging tolerance across species at both sites (Tadham,  $r = 0.82$ ,  $n = 64$ ,  $P < 0.0001$  (Fig. 2a); Cricklade,  $r = 0.98$ ,  $n = 51$ ,  $P < 0.0001$  (Fig. 2b)), indicating a trade-off between tolerances.

We used the method of phylogenetically independent contrasts, as implemented in the computer program CAIC<sup>19</sup>, to check the robustness of the trade-off between drought and waterlogging tolerance (Fig. 2). A composite phylogeny (available from the authors), with branch lengths set equal, was constructed for the 83 species in the study by using the most up-to-date molecular phylogenies available. Regression through the origin of aeration and dryness SEV contrasts gave a highly significant negative relationship at both sites (Tadham,  $y = -1.20x$ ,  $F_{(1,52)} = 87.12$ ,  $P < 0.0001$ , adjusted  $R^2 = 0.62$ ; Cricklade,  $y = -1.68x$ ,  $F_{(1,44)} = 1,279$ ,  $P < 0.0001$ , adjusted  $R^2 = 0.966$ ). The trade-off between soil-drying and waterlogging tolerance is therefore not only strong, but has shaped the evolution of tolerances in many independent cases<sup>20</sup>.

For at least two reasons, meadows are unlikely to be the only species-rich communities that are structured by segregation of species along niche axes of soil drying and soil aeration. First, segregation across topographic gradients has been observed in many plant communities, and we have shown that the spatial variation in hydrological conditions thought to cause this might occur in the absence of any obvious topographic variation (as at Tadham) and that plants are sensitive to hydrology at a fine scale. Second, the trade-off between drought and aeration tolerance that we have demonstrated here is so strong and phylogenetically robust that it cannot be confined to our set of species alone and must reflect a general physiological constraint with wide occurrence. The hitherto largely vain search for plant niches in the established phase of the plant life cycle has been confined mainly to axes of nutrients and light availability, but our findings suggest that investigations of variation in soil hydrology at a fine spatial scale and over longer time-spans might well reveal a potent force that structures many types of plant community. The precise mechanism by which this force acts now requires investigation. □

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## Ectoparasite infestation and sex-biased local recruitment of hosts

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Dispersal patterns of organisms are a fundamental aspect of their ecology, modifying the genetic and social structure of local populations<sup>1–4</sup>. Parasites reduce the reproductive success and survival of hosts and thereby exert selection pressure on host life-history traits<sup>4–6</sup>, possibly affecting host dispersal<sup>7–9</sup>. Here we test experimentally whether infestation by hen fleas, *Ceratophyllus gallinae*, affects sex-related recruitment of great tit, *Parus major*, fledglings. Using sex-specific DNA markers, we show that flea infestation led to a higher proportion of male fledglings recruiting in the local population in one year. In infested broods, the proportion of male recruits increased with brood size over a three year period, whereas the proportion of male recruits from uninfested broods decreased with brood size. Natal dispersal distances of recruits from infested nests were shorter than those from uninfested nests<sup>10</sup>. To our knowledge, this study provides the first evidence for parasite-mediated host natal dispersal and local recruitment in relation to sex. Current theory needs to consider parasites as potentially important factors shaping life-history traits associated with host dispersal.

As part of a long-term study on the evolutionary and ecological aspects of host–ectoparasite interactions<sup>11–13</sup>, we randomly infested half the nests in a population of great tits with adult hen fleas<sup>11</sup> over three breeding seasons. The remaining nests were kept free of fleas (see Methods). Similar to findings in another Swiss population<sup>14</sup>, flea infestation reduced the body mass of nestlings (mean mass ( $\pm$  s.e.) of 16-day-old nestlings: infested,  $15.19 \pm 0.16$  g; uninfested,  $15.84 \pm 0.15$  g; two-way ANOVA: flea treatment,  $F(1, 283) = 10.1$ ,  $P = 0.002$ ; year,  $F(2, 283) = 26.7$ ,  $P < 0.0001$ ; interaction, NS). Furthermore, the number of young fledged was lower in flea-infested than in uninfested broods (infested,  $4.0 \pm 0.2$ ,  $N = 162$  broods; uninfested,  $4.7 \pm 0.2$ ,  $N = 169$ ; two-way ANOVA for ranks: fleas,  $\chi^2_1 = 7.28$ ,  $P = 0.007$ ; year,  $\chi^2_2 = 4,015$ ,  $P < 0.0001$ ; interaction, NS). Thus, flea infestation had detrimental effects on great tit reproduction during the nestling period.

During the three years of the experiment, uninfested broods ( $N = 150$ ) fledged 797 young of which 63 (7.9%) were recaptured as first-time breeders (that is, recruits; see Methods). Infested broods ( $N = 137$ ) fledged 654 young of which 48 (7.3%) were recruited. Flea infestation had no significant effect on the total proportion of broods recruiting young (log likelihood ratio: fleas,  $\chi^2_1 = 0.34$ ,