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Research article

Convergent succession of plant communities is linked to species' functional traits

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ABSTRACT

Functional traits reflecting the resource economy and growth strategy of plants vary widely both within and among ecosystems. Theory suggests that trait variation within a community may determine the relative abundance of species, though this idea requires more empirical support.

We set up a long-term succession experiment in a nutrient-poor wetland, planting seedlings of twelve fenland species in different relative abundances and absolute densities, thereby creating 24 communities. The biomass of these species and the soil water and nutrient status of the system were monitored over ten years. Using these data, we could relate the changing relative abundance of species to five traits – leaf dry matter content (LDMC), leaf nitrogen concentration (LNC), specific leaf area (SLA), relative growth rate (RGR), and seed mass (SM).

The initial communities converged after ten years to a common dominance–diversity structure, with two species accounting for 82% of total biomass. Soil water and nutrient conditions remained largely constant. By the end of the experiment, community trait structure had changed so that species functional traits were significantly related to their relative abundance. The most abundant species had high LDMC and SM, but low RGR and SLA, and varied little in LNC, suggesting that investment in leaf structure and retention of nutrients were most important for species dominance under low nutrient conditions. Our results provide experimental evidence that dominance–subdominance structures in plant communities are governed by functional traits.

Introduction

The processes of dispersal, growth, and reproduction are strongly influenced by the functional traits of plants (Grime, 1998). These traits vary widely, not only among biomes, but also within communities (Diaz et al., 2004; Wright et al., 2004), where they may determine the relative abundance of different species. Three traits have received particular attention because they closely reflect the resource economy and growth strategy of species; these are: (i) leaf nitrogen content (LNC), because the proteins involved in the photosynthesis account for a large proportion of this resource (Wright et al., 2004), (ii) specific leaf area (SLA), which affects the efficiency with which leaves capture light and carbon dioxide (Vendramini et al., 2002), and (iii) leaf dry matter content (LDMC), which reflects a plant's investment in persistent leaf structures and therefore in nutrient retention (Ryser and Urbas, 2000; Wright and Cannon, 2001). Under low light, SLA is correlated to the relative growth rate (RGR) of plants (Shipley, 2006); further, RGR itself has been (positively) correlated to biomass production in communities (Vile et al., 2006). Overall, these few traits characterise a spectrum of strategies ranging from fast growing species with high biomass turnover and rapid nutrient acquisition to slow growing species with permanent leaf structures and efficient conservation of nutrients (Westoby et al., 2002; Wright et al., 2004).

Many studies indicate that the growth strategy of a species relative to that of competing species affects its proportional contribution to the vegetation (Campbell and Grime, 1992; Weiher and Keddy, 1995; Harpole and Tilman, 2006), and there is also evidence for a tight link between the trait structure of a plant community and ecosystem properties (Lavorel and Garnier, 2002; Garnier et al., 2004; Hooper et al., 2005). However, there is much less evidence linking plant traits to the relative abundance of species within communities over longer time-scales, and relating these links to (potentially changing) ecosystem properties over time. Such evidence, were it to emerge, would make it possible to predict changes in ecosystem processes during succession from observed changes in functional traits. For example, Garnier et al. (2004) demonstrated that changes in soil nutrient status of grasslands along a forty year chronosequence were correlated with changing values of LDMC,

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LNC, and SLA in the vegetation. The authors determined the interrelationships between traits and ecosystem properties on the basis of all species present, but the question of whether the relative abundance of individual species in the vegetation was influenced by their functional traits was not considered.

In this paper, we investigate the link between a small set of functional traits and the changing relative abundance of plant species in experimental communities. The experiment was started in 2001, when about 6000 seedlings from twelve fenland species were planted in differing proportions into 24 stands. Changes in species abundance were then monitored over the next ten years. In a previous paper we showed that the main driver of relative abundance during the first few years was species identity, with fast growing species (measured as the relative biomass production from year to year) becoming dominant (Suter et al., 2010). However, given the low nutrient conditions at the site, we hypothesised that as the succession proceeded an ability to retain nutrients would become more important than fast growth (Aerts and Chapin, 2000).

Here we analyse the species abundance data in relation to the changing importance of five species traits: LDMC, LNC, SLA, RGR, and seed mass (SM; included because new individuals established from seed during the experiment). In light of the established gradient of species' growing strategies (Diaz et al., 2004; Wright et al., 2004), we assessed whether a shift in community trait structure had occurred and, if so, whether it was related to changes in ecosystem-level properties such as soil nutrients and water conditions. Specifically, the following questions were addressed:

(i) Does the decade-long succession of initially differing communities lead to a common abundance structure of species?
(ii) Does community trait structure change over time and, if so, which traits dominate communities at different stages?
(iii) Can the dominant traits in communities be related to changing soil nutrient and soil moisture conditions in the ecosystem?
(iv) Which traits govern species abundance? Given the established gradient of growing strategies, we predicted high LNC, SLA, and RGR would be initially important, while the importance of high LDMC would increase over time.

Materials and methods

Plant species and design of experiment

A full description of the experimental set-up is given in Suter et al. (2010). The design consisted of six initial plant communities that differed in the relative abundance of twelve species; each initial community was planted at two densities, and each combination of community and density was replicated twice. The 24 stands were arranged in a completely randomised design.

The experiment was established in May 2001 at a field site in Northern Switzerland (N 47°36′52″, E 8°50′1″). The soil of the site was peaty with a pH of 6.3 ± 0.02 (mean ± SE across all stands). Plants were perennial fenland species common in Central Europe, and varied widely in growth form (taxonomic group in parentheses). They were tussock species: *Carex elata* (sedge), *Carex flava* (sedge), *Juncus effusus* (rush), *Molinia caerulea* (grass); upright species (all forbs): *Angelica sylvestris*, *Epilobium parviflorum*, *Lythrum salicaria*; rosette species (all forbs): *Centaurea jacea* spp. *angustifolia*, *Myosotis nemorosa*, *Silene flos-cuculi*; and stoloniferous species (all forbs): *Lycopus europaeus*, *Mentha aquatica* (nomenclature following Aeschimann and Heitz, 2005). Seedlings of all species were grown up from seeds in spring 2001.

Communities were planted in a high (HD) and a low (LD) overall density of 360 and 132 seedlings, respectively, with all twelve species being initially present in each stand. Communities contained either equal numbers of individuals of each species (HD: 30, LD: 11) or had one species as a dominant (HD: 129 of one species, 21 of others; LD: 44 of one species, 8 of others). To prevent the experiment becoming too large, only *C. elata*, *C. flava*, *L. europaeus*, *L. salicaria*, and *M. aquatica* were selected as dominants. The plots were 2.0 m × 2.0 m, and individuals were planted in a hexagonal array with a spacing of either 12 cm (HD) or 20 cm (LD). One species, *E. parviflorum*, disappeared after one year and was omitted from the analyses.

Maintenance and measurements in the field

Over the ten years of observations, the planted species were allowed to recruit naturally from seed. Any plants of other species that established were removed, though from 2005 onward this was scarcely necessary. Unless otherwise stated, all plots were mown in late October at 10 cm above ground surface, and the cut material was removed, thereby simulating the typical management of fen meadows in Central Europe.

The communities were monitored each year in late summer (August or early September). In 2001, species abundance was measured non-destructively using the point-intercept method (Stampfli, 1991), and in 2003 the aboveground biomass was harvested (Suter et al., 2010). From 2005 onward, biomass of species was assessed visually by the principal investigator (MS), with only the equal stands being evaluated in 2005 and 2006. In 2010, the equal stands were assessed visually and the aboveground biomass was then harvested to calibrate the visual assessment. The coefficients of determination (r^2) between harvested and visually assessed data pooled over all plots were 0.93 and 0.94 on linear and log scales, respectively; from these results we concluded that the visual assessments were accurate enough to quantify community development (for a more detailed analysis see Appendix A).

The groundwater level in each plot was measured at monthly intervals during the growing season (April–October) in all years except 2004. Potential effects of soil nutrients on communities were investigated by taking soil samples from each plot in October 2010 and determining their contents of inorganic and total nitrogen, phosphorus, and carbon, thereby repeating analyses done in 2001 (Suter et al., 2010). As in 2001, the 2010 data revealed homogenous conditions within the experimental field, with no differences that could be related to species relative abundance in either water or nutrient conditions (for detailed methods and results on the analyses on soil water and nutrients see Appendices B and C).

Measurements on plant traits

Leaf dry matter content (LDMC, ratio of leaf dry mass to fresh weight), leaf nitrogen concentration (LNC), and specific leaf area (SLA, ratio of leaf area to leaf dry mass) were determined for ten individuals per species. For this, young mature leaves were collected from the site in June and July 2010, with plants being selected by stratified random sampling from stands with differing initial planting conditions (stands with high and low planting density; species being either equal, dominant, or subdominant at the start). LDMC was determined following the protocol of Vendramini et al. (2002), with samples being collected in early morning and stored in sealed and moistened plastic bags that were kept in cooling boxes during transport. In the laboratory, the leaves were blotted dry with tissue paper and their fresh weights determined on the day of collection; they were then dried at 75 °C to constant mass and reweighed. To determine LNC, air-dried plant material was milled and digested using the Kjeldahl procedure (100–150 mg