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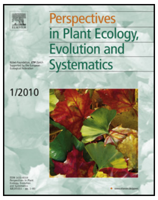

Research article

Convergent high diversity in naturally colonized experimental grasslands is not related to increased productivity

Christiane Roscher[a,b,*], Jens Schumacher[c], Jana S. Petermann[d,e,f], Alexander J.F. Fergus[d], Uta Gerighausen[g], Stefan G. Michalski[h], Bernhard Schmid[d], Ernst-Detlef Schulze[g]

[a] UFZ, Helmholtz Centre for Environmental Research, Physiological Diversity, Permoserstrasse 15, 04318 Leipzig, Germany
[b] German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5a, 04103 Leipzig, Germany
[c] Institute of Mathematics, Friedrich Schiller University Jena, Ernst-Abbe-Platz 2, 07743 Jena, Germany
[d] Institute of Evolutionary Biology and Environmental Studies and Zurich-Basel Plant Science Center, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland
[e] Department of Ecology and Evolution, University of Salzburg, Hellbrunnerstrasse 34, 5020 Salzburg, Austria
[f] Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany
[g] Max Planck Institute for Biogeochemistry, POB 100164, 07701 Jena, Germany
[h] UFZ, Helmholtz Centre for Environmental Research, Community Ecology, Theodor-Lieser-Strasse 4, 06120 Halle, Germany

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ABSTRACT

Initial plant diversity might control subsequent community assembly processes and plant productivity. To study these effects, we used a biodiversity experiment (Jena Experiment) with subplots of different sown diversity that were never weeded and spontaneously colonized control plots of different size (3.5 × 3.5 m, 20 × 20 m) with and without mowing in an 8-year study. On non-sown bare plots without mowing, colonizer accumulation depended on plot size resulting in a loss of diversity in large, undisturbed (unmown) control plots after initial colonization. On sown plots that were mown, species richness converged to high levels due to the accumulation of internal colonists (species belonging to the experimental pool of sown species), while initially high species richness of external colonists (species not belonging to the experimental pool) and residents (species sown on the plot) declined over time. The convergence of total species richness at higher levels was paralleled by increased taxonomic (Simpson index, Q_{Simp}), phylogenetic (Q_{Phylo}) and trait (FD_Q) diversity, whereby FD_Q was greatest on plots with low resident species richness after several years. Rates of change in terms of species colonization and extinction decelerated over time irrespective of resident species richness, mowing or plot size. While the contribution of residents declined and that of colonists increased, community biomass production did not change over time. The biomasses of residents and colonists were greatest at higher levels of species richness, partial Q_{Phylo} and FD_Q of the respective species group, but community biomass was consistently weakly related to total species richness and diversity indices. Our study shows that in contrast to the period of succession, "mature" plant communities resulting from natural assembly processes, favouring the coexistence of multiple species and thus high biodiversity, do no longer show significant relationships between species richness and variables related to ecosystem functioning such as primary productivity.

1. Introduction

The study of temporal dynamics of plant communities may help to identify the mechanisms determining community structure and diversity and its consequences for ecosystem functioning (Rees et al., 2001). Community assembly processes involve qualitative changes (i.e. in species occurrences) as well as quantitative changes (i.e. in species abundances). Rates of community change during succession often gradually decrease from rapid turnover during early stages of community assembly to a more stable compositional structure during later stages (Prach et al., 1993; Anderson, 2007). Because assembly processes result from many spatially dependent colonization and extinction events, the rate and patterns of succession may also depend on spatial factors (Glenn-Lewin et al., 1992). In this context, the theory of island biogeography (MacArthur and

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* Corresponding author at: German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5a, 04103 Leipzig, Germany.
E-mail address: christiane.roscher@ufz.de (C. Roscher).

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Wilson, 1967) may be considered a central framework related to the temporal development of plant communities. Large "islands" and those with a nearby source pool of potential colonists should have greater species richness than smaller or distant "islands" (Holt et al., 1995; Cook et al., 2005). Furthermore, extinction rates may be higher in small "islands" due demographic stochasticity and a greater risk of local extinction for small populations (Joshi et al., 2006). The probability of successful colonization is likely to decrease with increasing species richness because a greater fraction of the available species pool has already arrived.

Neutral theory (Hubbell, 2001) proposes that dispersal and demographic stochasticity are the primary mechanisms controlling assembly processes. It further assumes that all species are "functionally equivalent", resulting in local communities with temporally randomly varying species compositions if community equilibrium is achieved at equal immigration and extinction rates. From the point of view of the niche-based theory of community assembly (MacArthur and Levins, 1967), niche overlap among functionally similar species (limiting similarity) may inhibit the colonization of new species with similar resource acquisition strategies more strongly than the colonization of functionally more different species (Chesson, 2000). Under this scenario, local species richness is predicted to saturate and local communities are assumed to have similar species compositions due to deterministic assembly from the species pool (Chase, 2003). It has been suggested that a trade-off between colonizing abilities and traits related to competition are core to processes of succession (Tilman, 1988; Pickett and McDonnell, 1989). Species with high colonizing abilities will arrive faster, but their persistence depends on how fast they are replaced by later-arriving species with a greater competitive ability. Consequently, species diversity may also decline through time, when competition results in the dominance of a limited number of species (Whittaker, 1975; Mouquet et al., 2003). Competitive exclusion is more likely in stable, uniform environments, while periodic population reductions through moderate disturbance and environmental fluctuations may promote consistently high levels of diversity (Huston, 1979).

Approaches restricted to analyses of temporal changes in taxonomic (species) composition largely ignore ecological differences among the involved species. In recent years, it has been recognized that the comparison of phylogenetic and functional trait diversity with taxonomic diversity might be more insightful for separating the various mechanisms involved in community assembly processes (e.g. Gerhold et al., 2013; Purschke et al., 2013). For example, increasing and convergent levels of trait diversity through time would support the niche-based theory of community assembly, while decreasing levels of taxonomic and trait diversity may indicate weaker competitor exclusion. Because the quantification of trait diversity is based on a finite set of traits, it is assumed that phylogenetic diversity may cover a larger set of biologically relevant information (Webb et al., 2002). An increasing role of biotic interactions during community assembly may be reflected in decreasing phylogenetic relatedness among species. This is true if important functional traits are shared by species that have common ancestry or if phylogeny integrates information on biotic interactions, such as shared co-evolved enemies or mutualists, which is not covered by measurable functional traits (Cavender-Bares et al., 2009).

Guo (2003) suggested in a model based on data of natural plant succession that species richness–productivity relationships would change from positive via neutral to negative during succession because competition and competitive exclusion would decrease species richness while increasing productivity as a community "matures". In our study region, late-successional vegetation is dominated by shrubs and trees, while early-successional pioneer vegetation settling on open frequently disturbed places mainly consists of annual herbaceous species. Without disturbance the early-successional pioneer species are first replaced by perennial herbaceous species representing a mid-successional stage before the establishment of late-successional species (Whittaker, 1975). The long-term maintenance of mid-successional vegetation dominated by perennial herbaceous plant species such as grasslands depends on reoccurring moderate disturbances such as mowing or grazing (Ellenberg, 1988). For natural grasslands, the validity of the positive species richness–productivity relationship observed in many artificially maintained grassland biodiversity experiments has been repeatedly questioned (Thompson et al., 2005). Jiang et al. (2009) argued that differences in diversity–productivity relationships between immature experimental communities, where the diversity gradient is artificially maintained by weeding, and more mature natural communities are attributable to differences in species abundance patterns. In natural "mature" communities, it is more likely that rare species go extinct, while high productivity levels are maintained through dominant, highly productive species. In an earlier sub-experiment of the Jena Experiment we found that the removal of subdominant species from sown and weeded communities increased total community biomass (chapter 4 in Schmitz, 2007). Thus, the successional stage of the plant community may be a central factor for shifts in species richness–productivity relationships. Grassland biodiversity experiments are often established by sowing mid-successional temperate grassland species on bare ground and the experimental diversity gradient is maintained by regular weeding. Short-term studies in such biodiversity experiments with temperate mesophilic grassland species have shown that positive relationships between sown or total species richness and community biomass production were rapidly lost after cessation of weeding within two years at the Swiss Biodepth site (Pfisterer et al., 2004) or three years in the Jena Experiment (Petermann et al., 2010). Similar results were obtained in biodiversity experiments in subalpine grasslands (Rixen et al., 2008) and salt marsh (Doherty et al., 2011). The decay of positive species richness–productivity relationships was even faster when the natural colonization of new species was amended by seed addition (Petermann et al., 2010). The effects of sowing more species on biomass production have also been investigated in applied studies of grassland restoration on ex-arable land which did not weed unsown species after sowing. Studies restricted to two levels of sown diversity ("low" and "high" diversity) have shown that sowing more species enhances average productivity (Bullock et al., 2001; Lepš et al., 2007), but that particular low-diversity mixtures may reach similar productivity levels as high-diversity mixtures (Lepš et al., 2007).

In the present study, integrated into a large biodiversity experiment (Jena Experiment; Roscher et al., 2004), we established subplots which were never weeded after sowing, but regularly mown twice per year. In a previous analysis, encompassing the first two years after sowing (Roscher et al., 2009c), we showed that the species number of colonists and their immigration rates decreased, while their extinction rates increased with sown species richness and that total biomass production was initially positively related to sown species richness, but varied independently from total species richness of residents (sown species) plus colonists. The maturation of such unmanipulated communities could naturally lead to saturated communities with high productivity. However, it is also possible that these "maturing" communities do not achieve maximum productivity because productivity is primarily determined by the efficiency of carbon fixation and stand structure, i.e. leaf area index (Schulze et al., 2005), and community assembly processes starting from different initial compositions are not necessarily concordant with maximizing productivity. However, this has not been tested so far in a biodiversity experiment where the sown diversity gradient is not maintained by weeding because experimental plant communities are rarely followed for many years.