Theor Ecol (2009) 2:119–126
DOI 10.1007/s12080-008-0035-z

ORIGINAL PAPER

A unifying evolutionary theory for the biomass–diversity–fertility relationship

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Received: 3 March 2008 / Accepted: 28 November 2008 / Published online: 8 January 2009

Abstract Although a widely accepted ecological theory predicts that more diverse plant communities should be better able to capture resources and turn carbon dioxide into biomass, the most productive communities known are low diversity agricultural ones. This paradox has fuelled a long running controversy in ecology surrounding the nature of the relationship between diversity, productivity and fertility. Here, an evolutionary computer model is used which demonstrates that given the opportunity, species-rich communities may evolve under high fertility conditions. In contrast to low diversity, highly productive agricultural communities are shown to probably be a recent phenomenon. In simulations where fertility was applied to communities that had evolved under lower nutrient conditions, a few species had the ability to become 'dominant'. These species were responsible for the loss of diversity and for the majority of biomass production. These results are consistent with complementarity theory applying in nature in old co-evolved low nutrient communities, whereas in recently established fertile agricultural communities, dominant species appear to regulate biomass production. Understanding the nature of these 'dominant' species throws light on our understanding of phenotypic plasticity and the ecology of invasive species.

Keywords Biomass · Diversity · Ecological theory · Evolutionary theory · Fertility · Model

Introduction

There is a long running controversy in ecology (Craine 2007; Grime 2007; Tilman 2007) surrounding our understanding of the processes that regulate competition between plants. At the heart of this debate is the function of diversity and the relationship between biomass production and species richness. After years of research, this remains one of the most controversial topics in ecology (Schwartz et al. 2000; Aarssen 2001; Herbert et al. 2004). Disagreement is so fundamental that it includes the very nature of this relationship, with some researchers reporting a positive relationship (Tilman et al. 1996; Hector et al. 1999; Loreau and Hector 2001a, b), whilst others claim that the highest levels of biomass production are associated with high fertility but low levels of diversity (Rusch and Oesterheld 1997; Grime 1998). A third group contend that there is no consistent relationship between yield and diversity (Hooper 1998; Kenkel et al. 2000). Of these contrasting opinions, the first has received most attention perhaps because it offers the attractive theoretical possibility for simultaneously enhancing agricultural production and biodiversity. The yield–diversity relationship must be a function of competition between species and life-history strategy differentiation. It has been argued (Loreau and Hector 2001a; Gross et al. 2007) that the

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The appendices files are currently available at http://www.irs.aber.ac.uk/oddox/.

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positive relationship between yield and diversity is a function of ‘complementarity’ between different species exploiting different resources by virtue of having different traits. As more species are added to a community, complementarity ensures that the efficiency of resources exploitation increases, effectively increasing the fertility of the system by increasing the amount of resources utilised and thus facilitating greater biomass production.

The alternate view argues that negative relationships occur between yield and diversity arise when dominant species (which become superior competitors as fertility increases) exclude less competitive and less productive species. This has been termed the ‘selection effect’ (Crawley et al. 1999; Turnbull et al. 1999; Rees et al. 2001). If this mechanism applies, then a few dominant species that possess particular significant traits will determine the abundance of subordinate species and thus regulate community functions. Indeed, subordinate species may be excluded from the community with little impact on biomass production or stability.

In nature, the relationship between biomass production and species level diversity observed over different sites with different levels of stress or nutrient has frequently been reported as hump-shaped (Bond 1983). More recently, this has been reported to occur during succession (Guo 2003); pioneer communities are low in diversity and productivity but with increased biomass production through succession, diversity will peak in mid-succession and fall as climax communities develop. The mechanisms driving the increasing phase of this relationship are uncontroversial (Rosenzweig 1995; Safford et al. 2001). In extremely stressful or low nutrient environments, only few species are able to survive and productivity is low. In contrast, the mechanisms which are responsible for the observed decline in species richness in highly productive communities are less well understood and are hotly debated in ecology (Grace 1991; Grime 1997). An important factor in understanding why high fertility is associated with low diversity in grasslands is the fact that such high levels of fertility are considered primarily the result of recent human activity (Smits et al. 2008). Of the many theories that have been proposed to explain this phenomenon, most fall into three camps; ecological explanations which invoke competitive exclusion as driving reduced diversity, evolutionary constraints which argue that diversity is limited by restricted ‘species pools’ and sampling/size effects that argue that as fertility rises, plant size increases so fewer individuals can occupy the same area and this effects squeezes out species by chance. In the sampling/size theory, diversity is positively correlated with fertility, but it occurs at larger spatial scales (Safford et al. 2001).

Much of the difficulty in understanding the biomass–diversity–fertility relationship arises because numerous factors are thought to be important and because several of these variables are likely to interact and be confounded in nature. These include historic chance of colonisation (Ejrnaes et al. 2006), environmental heterogeneity (Reynolds et al. 2007), different spatial scales applying in different sections of the fertility spectrum (Anderson et al. 2004), mycorrhizae (Klironomos et al. 2000), decomposition (Mazzoleni et al. 2007) and herbivory (Olofsson et al. 2008). Whilst being important in understanding the biomass–diversity–fertility relationship, the interactions between these variables make interpreting field data difficult. To avoid the complications that arise from field sites having different evolutionary and ecological histories here, we use an evolutionary ecological model of plant competition to investigate the nature of this relationship. Specifically, we investigate whether high fertility is associated with low diversity because such environments are of recent origin and diversity does not have the opportunity to establish or evolve or, alternatively, whether high fertility environments are incompatible with supporting high levels of diversity.

The model

The ‘Evolve’ vegetation model used has already been demonstrated to robustly simulate short-term community change and ecological processes (Warren and Topping 1999, 2004) and longer-term evolutionary mechanisms (Warren and Topping 2001). Full model details are available in the “Appendix” using a novel html documentation procedure to aid model communication which we have termed ODDox. In ODDox, model overview and details are combined using the ODD standard protocol for describing individual-based models (Grimm et al. 2006) and Doxygen (van Heesch 1997), a standard code documentation tool. This allows the model to be explored by following html links from general concepts to details of coding.

The model is not explicitly constructed of known ecological mechanisms but of simple mechanistic processes; however, many ecological patterns appear as emergent properties (Warren and Topping 1999, 2004). It operates by defining the growth, reproduction and deaths of individual plants by species-specific rules which can be considered as analogous to genes. These life-history traits are linked by ‘trade-off’ via a series of parameters which determine the capture and partitioning of resources within each individual. Individuals have no information about the competitive abilities of other individuals present. Competition arises within a three-dimensional arena for space and light above ground and resources below ground; hence, as individual plants grow, they directly modify their environment and thus indirectly interact with each other. Thus, tall plants ‘shade out’ shorter individuals; seedlings will not thrive adjacent to established plants because they are shaded and because of below-ground nutrient depletion. Reproduction occurs within defined seasons once individuals attain defined critical biomass. Although there is no plasticity altering the vegetative/reproductive ratio within a genotype, there is variation between genotypes in this respect. Cutting, grazing and disturbance are all incorporated in the model. Cutting removes material from all individuals above a defined height. Disturbance causes the death of randomly selected small patches of vegetation. Although grazing is random in selecting its potential location, it is subsequently selective because plants that allocate resources to defence are preferentially avoided. Simulations occur in monthly increments, the growth status of all individuals and state of the arena are recalculated at each step. The life-history rules are allowed to mutate when reproduction events occur, and long-term simulations of different arenas result in different species evolving and different plant communities developing. The model can therefore be used to investigate the various theories that vie to explain the decline in diversity with increased fertility.

Trade-offs within the model

Trade-offs are critical to the competitive relationships developed in the model and are necessary to prevent ‘runaway’ evolutionary advantages occurring. Nine trade-offs can be identified in the simulations. Two were implemented as binary choices: (a) prioritisation of either vertical or horizontal growth and (b) seed or vegetative reproduction. Two involved the distribution of finite resources between categories: (c) allocation of resources to reproduction, defence or growth and (d) allocation of resources to propagules, i.e. few large or many small. Two trade-offs were based on a determination of an optimum and range with linear relationships between optimum and range extremes: (e) pH tolerance, expressed as a maximum and minimum tolerable pH with an optimum mid-way between these and (f) resource extraction efficiency was determined by:

$$\mathrm{REEx} = 1 - |\mathrm{REE} - \mathrm{rs}|, \tag{1}$$

where REEx is the expressed resource extraction efficiency, REE is the innate extraction efficiency and rs is the resource level in the environment scaled to a range of 0–1.0. (g) Shade tolerance was traded off by reducing the utilisation of available light in full light conditions by the proportion of light gained under full shade conditions. (h) The maximum height an individual plant was able to grow determines whether it could shade other plants, but reproduction was prevented until the plant reached its maximum height; hence, an implicit trade-off exists between maximum height and time to reproduction. (i) A final implicit trade-off, linked to ‘h’ was between the size and age of the plant and the number of propagules. A plant with low leaf area could not gather resources for production of many propagules but could occupy small spaces, whereas large plants could produce many offspring after a longer period if able to occupy enough space to grow.

The simulations

Four sets of simulations were carried out to test if diversity can evolve under high fertility conditions. To do this, the relationship between diversity, biomass and fertility was investigated free from historic ecological differences or confounding between sites. The simulations were based on grazed grassland habitats of varying nutrient status because most of the field based studies of the biomass/diversity relationship are based on pasture systems (Table 1). In addition, the ability of diversity that evolved under low fertility conditions to persist when fertility was modified was investigated in a fifth set of simulations.

Table 1 Description of the five sets of simulations, outlining differences between the starting individuals, arenas and simulation durations

Simulation	Starting propagules	Below-ground resources	Reproductive strategy	Mutation rate	Simulation duration	Variable nutrient range
1	Mixed strategy	Homogeneous	Veg/seed	1 in 500	10,000	15–225
2	Mixed strategy	Heterogeneous	Veg/seed	1 in 500	10,000	15–225
3	Mixed strategy	Homogeneous	Seed only	1 in 500	10,000	15–225
4	Mixed strategy	Homogeneous	Veg only	1 in 500	10,000	15–225
5	Evolved in simulation 1 at N=75	Homogeneous	Veg/seed	None	100	15–225

In simulations 1 to 4, there were 100 propagules of each of the same six species of plants, based on typical grassland life-history strategies (two grasses, two forbs and two legumes)

The first four sets of simulations investigated the influence of different parameters each thought to be important in effecting diversity. Their effects on the level of diversity and biomass production within a specific environment were investigated. Each simulation of each arena was replicated ten times. Sets of simulations comprised of ten different arenas which varied in fertility status, ranging from very low fertility and limiting to growth and survival through to saturation levels (*N*=15 to 225 in arbitrary units of fertility). These were designed to mimic levels observed in real pasture communities from pioneer sand dunes to fertile improved agricultural pastures. All simulations were run for 10,000 years and all started with 100 propagules of each of the same six species of plants based on typical grassland life-history strategies (two grasses, two forbs and two legumes). Mutations in trait parameter values were allowed to occur in one of every 500 propagules; this may appear high but prior experience showed that mutation rate had no effect on the outcome of the simulations, just on the length of time before system stability was achieved.

In the first set of simulations, diversity was allowed to evolve in the different fertility arenas whilst being intensively grazed. The second set of simulations were identical to the first except that the soil nutrients were distributed randomly and heterogeneously across the arena at the start of each run rather than homogeneously as was the case in all other simulations. The third and fourth set of simulations were the same as simulation set 1, but here, species were restricted to being only seed reproducing (simulation 3) or only vegetatively reproducing (simulation 4). In simulation sets 1 and 2, seed reproducing and vegetative species were equally represented at the start and allowed to mutate between strategies during the simulations.

At the end of each simulation, the number of ‘species’ that had evolved during the simulation, the number remaining co-existing at the end and the annual biomass produced were recorded. Although defining the species concept at a genetic level is problematic (Rubinoff 2006), for simplicity, the model defines a ‘species’ as any individual differing by 5% or more in its life history traits from another.

A final set of simulations (simulation 5) using a limited pool of species that had co-evolved under low nutrient conditions investigated the effect of fertility on the diversity–biomass–fertility relationship when mutations were prevented. The starting ‘species’ used were derived from those co-existing at the end of simulation 1, at mid-fertility status (*N*=75). These ‘species’ were transplanted separately from the end of each of the ten (*N*=75) replicates of simulation 1 into the start of ten sets of simulation 5. Simulations again started with 100 propagules of all species growing in the full range of homogeneous nutrient arenas and allowed to compete for 100 years. As before, each set of simulations occurred over the full range of fertility conditions and were replicated ten times. This procedure was performed separately for each set of co-existing species which evolved in the ten (*N*=75) replicates of simulation 1.

Results

The key results to emerge from our simulations are:

1. In simulation sets 1 to 4, when diversity (defined as the final number of co-existing species) was given equal opportunity to evolve across a range of different fertility levels, a positive relationship between fertility status and diversity emerges, with no evidence of diversity declining at high fertility (Fig. 1). Two-way analysis of variance (ANOVA) of these data revealed a highly significant effect of fertility on species richness ($P<0.001$). Across all four simulations at extremely high ($N=400$) levels, there were no significant difference in diversity from $N=200$, indicating diversity had plateaued (results not presented). At low fertility levels, diversity levels were lower, but rates of evolution were faster, so that by the end of the 10,000 years in simulation 1, an average of 55,681 ‘species’ has occurred at low fertility status compared with the significantly lower average of 31,228.6 ‘species’ in the highest nutrient levels ($P<0.001$ one-way ANOVA). Total biomass production increased linearly with fertility (Fig. 2) in a remarkably tight relationship, although the correlation was less clear in simulation 4.

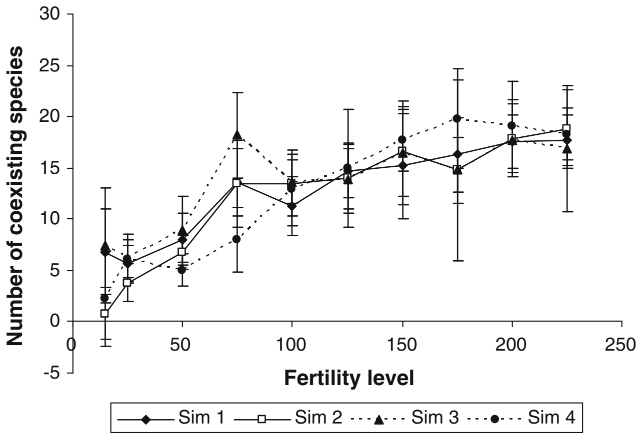

Fig. 1 The relationship between diversity and fertility under different environmental conditions, expressed as the average number of ‘species’ that are able to co-exist after 10,000 years over ten replicates (± standard deviation) in each of the ten fertility status arenas, in four simulated environments) in each of the ten fertility status arenas, in four simulated environments

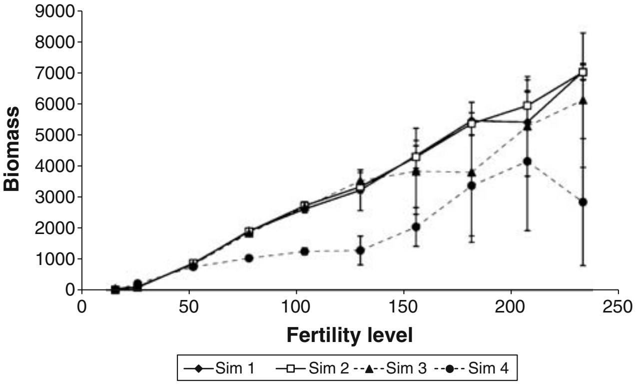

Fig. 2 The relationship between biomass production and fertility under different environmental conditions, expressed as the average biomass produced by all the plants present in June after 10,000 years over ten replicates (± standard deviation) in each of the ten fertility status arenas, in four simulated environments

2. The two-way analysis of variance of species richness in simulations 1 to 4 revealed no significant difference in diversity between simulations. Environmental heterogeneity had no noticeable effect on promoting diversity. Although restricting the dispersal powers of plants (simulation 4, vegetative reproduction) appeared to promote slightly higher levels of diversity, this was not significant.
3. In simulation 5 (the transplant experiment), for the most part, plants that had co-evolved in moderate fertility conditions were able to continue to co-exist when they were mutually transplanted into a high fertility environment (Fig. 3), and they maintained their short phenotypes (Fig. 4). However, in one of the ten replicates, a potentially 'dominant species' evolved in simulation 1 that was able to grow tall and outcompete many of its co-evolved species when they were transplanted into a high fertility arena (Figs. 3 and 4). Additional replicates (results not presented) suggest that dominant species in simulation 5 evolve at a probability of 5–10% in simulation 1.

Discussion

At the heart of the long running controversy surrounding the relationship between biomass, diversity and fertility is the uncertainty surrounding the low levels of diversity associated with high fertility. Is species richness limited by the lack of opportunity for it to evolve or is high diversity incompatible with high nutrient status and high biomass production (Smits et al. 2008)? The simulation results presented here suggests that if sufficient time is available, then diversity may evolve under high fertility conditions.

The long-term simulations (1–4) show no indication of the humped back relationship between diversity and fertility. When given the opportunity, species-rich communities always evolved under high fertility conditions whatever the other environmental constraints. In simulations 1 to 4, high fertility was associated with high diversity and biomass production, with many species contributing relatively equally to the production of biomass (Figs. 1 and 2). However, in simulation 5 when fertility was applied to communities that had evolved under lower nutrient conditions, sometimes certain species became 'dominant' (Figs. 3 and 4). These species were responsible for the competitive exclusion of other species and for the majority of biomass production and this phenomenon was responsible for generating the falling section of the hump-backed relationship.

Simulations 1–4 are consistent with complementarity theory applying in all old co-evolved communities, irrespective of their nutrient status. However, in nature, evolution has only had opportunity to develop species-rich communities in low nutrient environments corresponding with the rising section humped-back relationship (Smits et al. 2008). In contrast, the high fertility section of simulation 5 represents newly established fertile agricultural communities. Here, dominant species may appear which

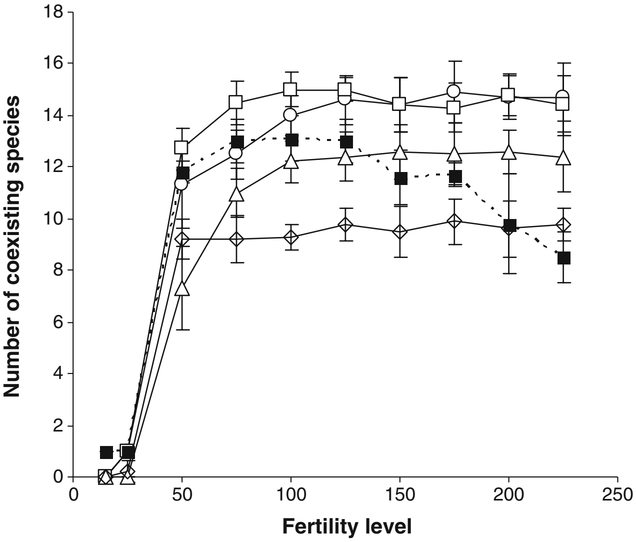

Fig. 3 Five replicates from simulation set 5. The average number of co-evolved 'species' from simulation 1 (N=75) that were able to continue to co-exists for a further 100 years when transplanted into different fertility environments (± standard deviation). In the replicates with *solid lines*, co-evolved 'species' were able to continue to co-exists; in the replicate with a *dashed line*, the evolution of a 'dominant species' resulted in the competitive exclusion of other species in the high fertility arenas

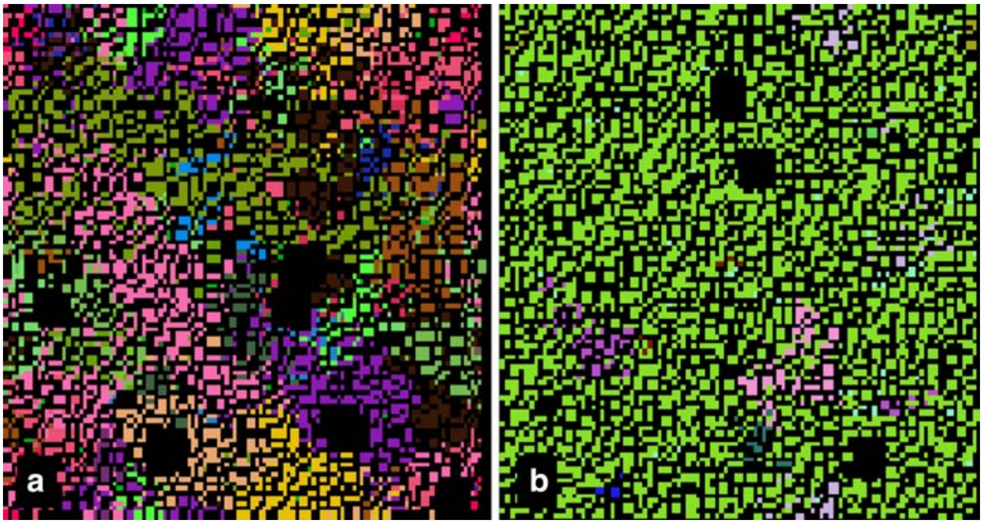

Fig. 4 **a** A typical two-dimensional representation of transplant simulation 5 after 100 years transplanted from N=75 to N=225, showing no evidence of a decline in diversity, with no ‘species’ with the ability to grow tall and become dominant. The *squares* represent a slice through the vegetation increasing close to ground level, each *colour* representing a different ‘species’. **b** A replicate of the same transplant experiment (simulation 5) based on different starting species that had co-evolved in a different replicate of simulation 1 at N=75 again transplanted to N=225. On this occasion, a potentially dominant ‘species’ with the ability to grow tall in the high N conditions had evolved and was successful in outcompeting many of its co-evolved species

regulate biomass production and the selection effect applies in what corresponds with the falling section of the humped-back relationship. We suggest therefore that both existing ecological theories are correct and may be unified. They apply to different communities with different evolutionary origins in different sections of the humped-back relationship.

In simulation 5, evolution was not allowed to occur, and thus, species complementarity could not develop. Under these conditions, chance seems to result in favouring a dominant species that contribute most to the production of biomass and which competitively exclude other species. Although in the majority of simulations, no dominant species were found. This observed variation between replicates (Fig. 3) may relate to the inconsistencies found in field data. Little weight can be attached to the frequency with which dominant species evolve as only relative small areas of vegetation were involved. Given the relatively small population sizes being modelled, it might be safe to assume that in life, potentially dominant species will always evolve.

Simulations 1 to 4 suggest that if high fertility conditions are maintained over long time periods, complementarity will evolve even in extremely fertile environments. This observation raises the interesting possibility that in the future, highly productive and diverse communities may be developed. However, given that seed set is rare in productive agricultural grasslands, this is unlikely to occur without human assistance.

The observation that low fertility conditions are associated with higher rates of species turnover and thus higher rates of evolution adds an additional complication to interpretation of the biomass–diversity–fertility relationship. We have argued that dominant species may regulate new communities where the erosion of their dominance has not yet had chance to evolve. It will therefore be difficult to compare diversity levels between communities if they are known to evolve at different rates.

Our observations suggest that species with the ability to become dominant in new environments (in this case high fertility) evolve by chance. Competitive superiority appears to relate to the ability to express a new phenotype when environmental conditions allow; this could be important in understanding the ecology of invasive species. Within our model, this phenotypic plasticity related to a species having ‘genes’ for growing tall that had evolved under moderate fertility; under these conditions, the trait could not be fully expressed because of environmental limitations. We have termed this phenomenon ‘asymmetric neutrality’ because mutations for growing short will be expressed and acted upon by selection, whereas tall mutants cannot express their full potential phenotype until the environmental constraints (limited nutrient availability) are removed, and thus, unexpressed ‘tall genes’ are selectively neutral until nutrients levels increase. If this asymmetric neutrality can be demonstrated in nature, it adds another dimension to Kimura’s neutral theory of evolution (Kimura 1983).

The surprising apparent failure of environmental heterogeneity to promote diversity (Fig. 1) results from the dynamic nature of soil nutrients over the long time scales involved. Within the simulations, environmental heterogeneity of below-ground nutrients was observed to develop within the homogeneous treatment (simulation 1) as nutrients were differentially exploited by the developing vegetation. Static environmental heterogeneity for soil pH and the role of limited dispersal in promoting diversity have previously been demonstrated by this model (Warren and Topping 2004). Such factors, although important in the ecology of the short term maintenance of diversity, appear less important in promoting the evolution of diversity than is fertility over longer time scales. Extra resources (fertility) equate to extra niches/opportunities to be exploited by additional species producing extra biomass, so long as evolution has time and genetic variation to produce these species.

Acknowledgements We thank Raj Whitlock, Chris Thomas, Peter Dennis and Jacob Weiner for advice and help with the manuscript. Chris Topping was supported by the Centre for Integrated Population Ecology.

References

Aarssen LW (2001) On correlations and causations between productivity and species richness in vegetation: predictions from habitat attributes. Basic Appl Ecol 2:105–114 doi:10.1078/1439-1791-00041

Anderson TM, McNaughton SJ, Ritchie ME (2004) Scale-dependent relationships between the spatial distribution of a limiting resource and plant species diversity in an African grassland ecosystem. Oecologia 139:277–287 doi:10.1007/s00442-004-1499-1

Bond W (1983) On alpha diversity and the richness of the cape flora: a study in southern Cape Fynbos. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds) Mediterranean type ecosystems: the role of nutrients. Springer, New York, pp 337–356

Craine JM (2007) Plant strategy theories: replies to Grime and Tilman. J Ecol 95:235–240 doi:10.1111/j.1365-2745.2007.01212.x

Crawley MJ, Brown SL, Heard MS, Edwards GR (1999) Invasion-resistance in experimental grassland communities: species richness or species identity? Ecol Lett 2:140–148 doi:10.1046/j.1461-0248.1999.00056.x

Ejrnaes R, Brunn HH, Graae BJ (2006) Community assembly in experimental grasslands: suitable environment or timely arrival? Ecology 87:1225–1233 doi:10.1890/0012-9658(2006)87[1225:CAIEGS]2.0.CO;2

Grace JB (1991) A clarification of the debate between Grime and Tilman. Funct Ecol 5:583–587 doi:10.2307/2389475

Grime JP (1997) The humped-back model: a response to Oksanen. J Ecol 85:97–98 doi:10.2307/2960631

Grime JP (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecol 86:902–910 doi:10.1046/j.1365-2745.1998.00306.x

Grime JP (2007) Plant strategy theories: a comment on Craine (2005). J Ecol 95:227–230 doi:10.1111/j.1365-2745.2006.01163.x

Grimm V, Berger U, Bastiansen F et al (2006) A standard protocol for describing individual-based and agent-based models. Ecol Model 198:115–126 doi:10.1016/j.ecolmodel.2006.04.023

Gross N, Suding KN, Lavorel S, Roumet C (2007) Complementarity as a mechanism of coexistence between functional groups of grasses. J Ecol 95:1296–1305 doi:10.1111/j.1365-2745.2007.01303.x

Guo QF (2003) Temporal species richness–biomass relationships along successional gradients. J Veg Sci 14:121–128 doi:10.1658/1100-9233(2003)014[0121:TSRRAS]2.0.CO;2

Hector A et al (1999) Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127 doi:10.1126/science.286.5442.1123

Herbert DA, Rastetter EB, Gough L, Shaver GR (2004) Species diversity across nutrient gradients: an analysis of resource competition in model ecosystems. Ecosystems (N Y Print) 7:296–310 doi:10.1007/s10021-003-0233-x

Hooper DU (1998) The role of complementarity and competition in ecosystem responses to variation in plant diversity. Ecology 79:704–719

Kenkel NC, Peltzer DA, Baluta D, Pirie D (2000) Increasing plant diversity does not influence productivity: empirical evidence and potential mechanisms. Community Ecol 1:165–170 doi:10.1556/ComEc.1.2000.2.6

Kimura M (1983) The neutral theory of molecular evolution. Cambridge University Press, New York

Klironomos JN, McCune J, Hart M, Neville J (2000) The influence of arbuscular mycorrhizae on the relationship between diversity and productivity. Ecol Lett 3:137–141 doi:10.1046/j.1461-0248.2000.00131.x

Loreau M, Hector A (2001a) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76 doi:10.1038/35083573

Loreau M, Hector A (2001b) Partitioning selection and complementarity in biodiversity experiments. Nature 413:548–548 doi:10.1038/35097128

Mazzoleni S, Bonanomi G, Giannino F et al (2007) Is plant biodiversity driven by decomposition processes? An emerging new theory on plant diversity. Community Ecol 8:103–113 doi:10.1556/ComEc.8.2007.1.12

Olofsson J, de Mazancourt C, Crawley MJ (2008) Spatial heterogeneity and plant species richness at different spatial scales under rabbit grazing. Oecologia 156:825–834 doi:10.1007/s00442-008-1038-6

Rees M, Condit R, Crawley M, Pacala S, Tilman D (2001) Long-term studies of vegetation dynamics. Science 293:650–655 doi:10.1126/science.1062586

Reynolds HL, Mittelbach GG, Darcy-Hall TL et al (2007) No effect of varying soil resource heterogeneity on plant species richness in a low fertility grassland. J Ecol 95:723–733 doi:10.1111/j.1365-2745.2007.01252.x

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press, New York

Rubinoff D (2006) Utility of mitochondrial DNA barcodes in species conservation. Conserv Biol 20:1026–1033 doi:10.1111/j.1523-1739.2006.00542.x

Rusch GM, Oesterheld M (1997) Relationship between productivity, and species and functional group diversity in grazed and non-grazed Pampas grassland. Oikos 78:519–526 doi:10.2307/3545613

Safford HD, Rejmanek M, Hadac E (2001) Species pools and the “hump-back” model of plant species diversity: an empirical analysis at a relevant spatial scale. Oikos 95:282–290 doi:10.1034/j.1600-0706.2001.950210.x

Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. Oecologia 122:297–305 doi:10.1007/s004420050035

Smits NAC, Willems JH, Bobbink R (2008) Long-term after-effects of fertilisation on the restoration of calcareous grasslands. Appl Veg Sci 11:279–292

Tilman D (2007) Resource competition and plant traits: a response to Craine et al. 2005. J Ecol 95:231–234 doi:10.1111/j.1365-2745.2007.01201.x

Tilman D, Wedin D, Knops J (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379:718–720 doi:10.1038/379718a0

Turnbull LA, Rees M, Crawley MJ (1999) Seed mass and the competition/colonization trade-off: a sowing experiment. J Ecol 87:899–912 doi:10.1046/j.1365-2745.1999.00405.x

van Heesch D (1997) Doxygen. www.doxygen.org

Warren JM, Topping CJ (1999) A space occupancy model for the vegetation succession that occurs on set-aside. Agric Ecosyst Environ 72:119–129 doi:10.1016/S0167-8809(98)00168-6

Warren J, Topping CJ (2001) Trait evolution in an individual-based model of herbacious vegetation. Evol Ecol 15:15–35 doi:10.1023/A:1011936121454

Warren J, Topping CJ (2004) A trait specific model of competition in a spatially structured plant community. Ecol Model 180:477–485 doi:10.1016/j.ecolmodel.2004.04.033