ESSAY REVIEW

Benefits of plant diversity to ecosystems: immediate, filter and founder effects

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Summary

1 It is useful to distinguish between the immediate effects of species richness on ecosystems and those which become apparent on a longer time scale, described here as filter and founder effects.

2 Relationships between plant diversity and ecosystem properties can be explored by classifying component species into three categories – dominants, subordinates and transients. Dominants recur in particular vegetation types, are relatively large, exhibit coarse-grained foraging for resources and, as individual species, make a substantial contribution to the plant biomass. Subordinates also show high fidelity of association with particular vegetation types but they are smaller in stature, forage on a more restricted scale and tend to occupy microhabitats delimited by the architecture and phenology of their associated dominants. Transients comprise a heterogeneous assortment of species of low abundance and persistence; a high proportion are juveniles of species that occur as dominants or subordinates in neighbouring ecosystems.

3 A 'mass ratio' theory proposes that immediate controls are in proportion to inputs to primary production, are determined to an overwhelming extent by the traits and functional diversity of the dominant plants and are relatively insensitive to the richness of subordinates and transients. Recent experiments support the mass ratio hypothesis and the conclusion of Huston (1997) that claims of immediate benefits of high species richness to ecosystem functions arise from misinterpretation of data.

4 Attribution of immediate control to dominants does not exclude subordinates and transients from involvement in the determination of ecosystem function and sustainability. Both are suspected to play a crucial, if intermittent, role by influencing the recruitment of dominants. Some subordinates may act as a filter influencing regeneration by dominants following major perturbations.

5 Transients originate from the seed rain and seed banks and provide an index of the pool of potential dominants and subordinates at specific sites. Where the landscape carousel operates against a background of declining diversity in the reservoir of colonizing transients, we may predict that a progressive loss of ecosystem functions will arise from the decline in the precision with which dominants can engage in the re-assembly and relocation of ecosystems.

Keywords: biodiversity, dominance, ecosystem function, landscape ecology, regeneration

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Introduction

When ecosystems become degraded by pollution or over-exploitation to a point where formerly dominant organisms are eliminated or debilitated, it is often possible to demonstrate a causal connection between losses in biodiversity and declines in ecosystem function and in benefits to humans (Smith 1968; LeCren *et al.* 1972; Pearson & Rosenberg 1976; Vitousek & Melillo 1979). A more difficult subject for analysis arises in circumstances where either species-poor eco-

systems (e.g. boreal forests, bogs and heathland) or species-rich ecosystems (e.g. limestone grasslands, tropical forests and coral reefs) remain in existence but experience gradual losses in species or genetic diversity (Thomas 1960; Bobbink & Willems 1987; Barr *et al*. 1993). Does such attrition, particularly where it affects species of low relative abundance in communities, have major implications for ecosystem function and viability?

To address this question it is helpful to recognize two separate issues. First, we need to know whether losses in species richness have immediate (proximal) effects on ecosystem function. Secondly, it is necessary to consider the possibility of less conspicuous long-term consequences. This paper comments briefly on both issues. Evidence is drawn mainly from studies of herbaceous vegetation but there appear to be some principles that apply more widely.

Dominants, subordinates and transients

In order to estimate the consequences of a species loss upon its host ecosystem, it is necessary to know what role (if any) the organism concerned plays within it (Grime 1973; Whittaker 1975; McNaughton 1978; Lawton 1994). In his pioneering attempts to define the functional roles of species within plant and animal communities, Whittaker (1965, 1975) recognized that a useful first step is to order component species according to their relative abundance or productivity. When large numbers of the resulting 'dominance–diversity' profiles are constructed it is possible to begin the search for consistent associations between the traits of species and their abundance in ecosystems and communities.

For European herbaceous vegetation, there is an enormous fund of information on the abundance and characteristics of component species in relatively small (*c*. 1 m^2) vegetation samples. Discussions of the functional significance of these data are available in Grime (1973, 1987), Grubb *et al*. (1982) and Mitchley & Grubb (1986). Many ecological factors and plant traits deserve consideration as potential determinants of dominance–diversity profiles, and it is clear that controlling effects vary in detail from site to site. However, a generalization can be attempted and this is summarized in Fig. 1 in the form of an idealised dominance–diversity curve (*sensu* Whittaker 1965). This suggests that within the majority of herbaceous vegetation samples three elements can be recognized, each capable of varying in species richness and taxonomic identity, and here described as dominants, subordinates and transients. The dominants are usually few in number, taller and more expansive in morphology and account for a high proportion of the biomass (as seen for a grassland example in Fig. 2). Many subordinates consistently co-occur with particular dominants and, although they are usually more numerous as individuals than the dominants, they are

smaller in stature (Fig. 2) and form a lower proportion of the biomass. In marked contrast to the subordinates, the transients are heterogeneous and lack fidelity of association with particular dominants. They make a very small total contribution to the vegetation and vary in number and in functional traits to a great extent. Most are represented only as seedlings or juveniles and a high proportion are species that occur as dominants or subordinates in other ecological situations (Table 1) often situated nearby. In passing, it is interesting to note that formal procedures used to collect and analyse data on the species composition of plant communities (e.g. Clements 1905; Braun-Blanquet 1932; Bray & Curtis 1957; Kent & Coker 1992) often have the effect of under-recording or discarding information on transients which, from a classificatory viewpoint, are frequently regarded as 'misfits'. Table 1 shows that such excursions by species appear commonplace when detailed and exhaustive sampling procedures are applied: records from all three of the sampled habitats include many species that are more typically associated with other habitats.

Immediate effects of biodiversity

Can we generalize about the relative importance of dominants, subordinates and transients as determinants of ecosystem properties such as productivity, carbon sequestration, water relations, nutrient cycling and storage, litter quality and resistance and resilience to perturbations? Both theory and experimental evidence (Huston 1997; Aarssen 1997) suggest that the extent to which a plant species affects ecosystem functions is likely to be closely predictable from its contribution to the total plant biomass. This 'mass ratio' hypothesis is implicit in many commentaries and models relating to ecosystem function (Shugart 1984; Pastor & Post 1986; Huston & Smith 1987; Grime 1987; Sala *et al*. 1996; Huston 1997) and is dictated by the laws of physics and chemistry that require that large effects of autotrophs within ecosystems involve major participation in syntheses, and in inputs to resource fluxes and degradative processes. It follows that ecosystem properties should be determined to a large extent by the characteristics of the dominants and will be relatively insensitive to variation in species richness in circumstances where this is attributable to changes in the number of subordinates and transients. It is important to specify that the mass ratio hypothesis is restricted in application to the role of autotrophs in ecosystem processes. When attention is turned to other trophic elements, such as parasites, herbivores, predators and symbionts, the possibility arises for ecosystem impacts that are less predictably related to abundance.

A growing body of experimental evidence supports the hypothesis that ecosystem properties are strongly influenced by the characteristics of dominant plants. In a comparative study of the resistance and resilience
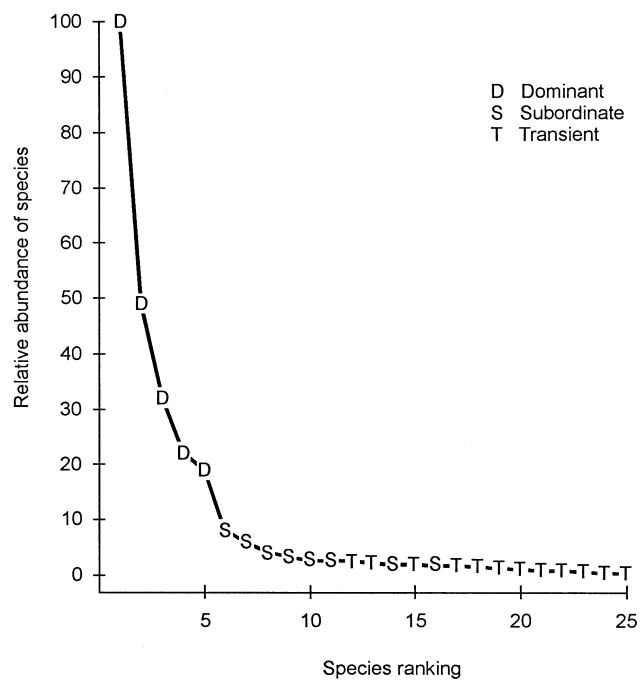
Fig. 1 An idealised dominance–diversity curve (*sensu* Whittaker 1965) for a small sample of herbaceous vegetation. The distinction between dominants and subordinates is based upon relative abundance and has been set at an arbitrary value (10%). Transients are distinguished from subordinates by their failure to regenerate and persist in the vegetation under scrutiny.

of five herbaceous communities to drought, late frost and fire (MacGillivray *et al.* 1995), predictions using traits measured in the laboratory were found to be accurate when calculations were based upon means weighted according to the relative abundance of each plant species at each experimental site. A similar conclusion was drawn from two recent investigations (Wardle *et al.* 1997; Hooper & Vitousek 1997) in which various ecosystem properties were found to be strongly correlated with the functional characteristics of the dominant contributors to the biomass.

There is also strong evidence that functional differences between co-existing dominants can have profound effects on ecosystems, particularly in sustaining yield over periods in which there is fluctuation in climate or vegetation management. From both monitoring studies and experiments (Willis 1963; Mellinger & McNaughton 1975; Kemp & Williams 1980; Grime *et al.* 1985) there is abundant evidence that differences occur between codominants, in phenology, photosynthetic mechanism, rooting depth and reproductive biology. In some reported cases (Spedding & Diekmahns 1972; Armstrong & Eadie 1973; Hooper & Vitousek 1997) such complementary exploitation has been shown to confer a benefit to productivity.

If the immediate influence of vegetation on the properties of ecosystems is determined primarily by traits of the dominants, it is necessary to consider what additional effects might be exerted by subordinates and transients. First, perhaps, it should be noted that there is no a priori reason to suspect that such minor contributors must influence ecosystem

functioning; their presence may simply reflect the fact that conditions prevailing in the past or present have allowed them to be admitted. However, several sources of evidence suggest that some subordinate members of plant communities (as distinct from transients) fulfil roles that extend beyond that of mere adventives. We may suspect that the consistent associations evident between certain dominants and their subordinates (e.g. Fig. 2) reflect a complementary exploitation of habitat resulting in a more complete capture of resources and minor benefits to productivity. In some pairings of subordinates with dominants, spatial and temporal interlocking finds precise morphological expression, as in the case of the bryophyte *Brachythecium rutabulum* which, in winter, colonizes each fallen stem of the litter of the tall herb *Urtica dioica* (Furness & Grime 1982). More often complementarity between dominants and subordinates consists of circumstances in which the latter exploit relatively unfavourable microhabitats. These may be expressed spatially, as in the case of the creeping herbs and bryophytes that occupy the shaded lower strata of herbaceous canopies (Al-Mufti *et al.* 1977; Fig. 2), or temporally, as exemplified by the small winter annuals and spring geophytes that make a minor contribution to the biomass of species-rich calcareous grasslands (Ratcliffe 1961; Grime *et al.* 1985).

Further evidence of mechanisms of habitat exploitation complementarity between dominant and subordinate members of a plant community is available from an experiment (Campbell *et al.* 1991) in which the abundance of eight plant species in an exper-
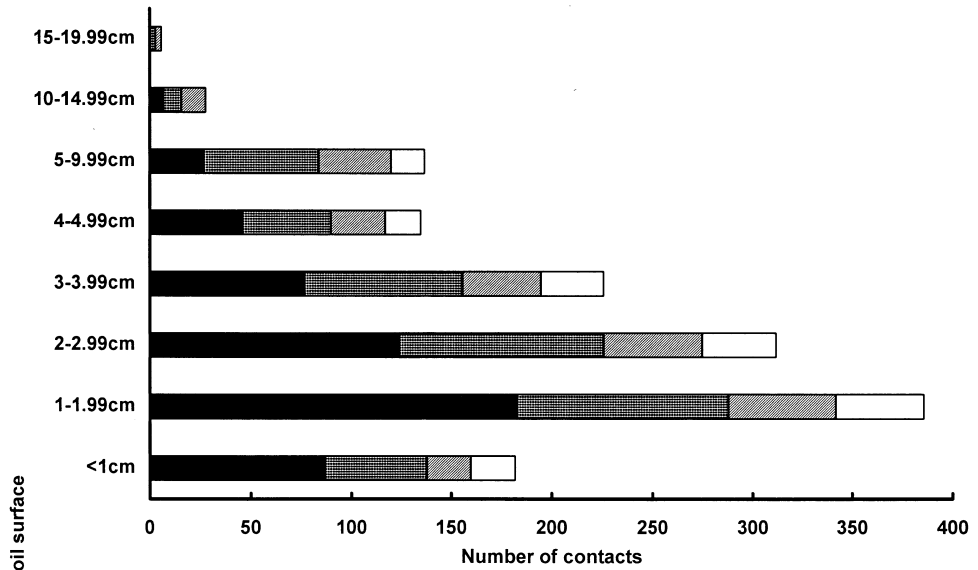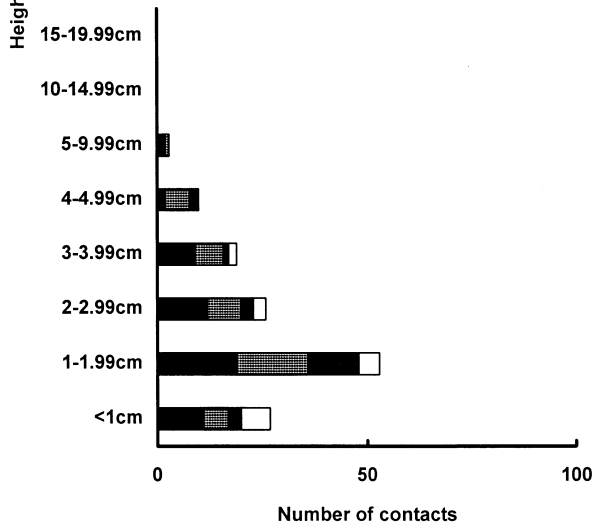
Fig. 2 Vertical distribution of the leaf canopy of (a) four selected dominant and (b) four selected subordinate component species in an ancient limestone pasture at Buxton, North Derbyshire, UK. Canopy distribution in June was estimated by measuring contacts with 375 randomly distributed, vertical pins (S. H. Hillier, unpublished data).

Table 1 Ecological classification of the species recorded in three distinctive and highly contrasted habitats sampled widely in an area of 2400 km^2 around Sheffield, UK. All the species encountered within a particular habitat were classified in terms of their primary habitat (columns 3–6). Details of the sampling, recording and habitat classification procedures are provided in Grime *et al.* (1988)

Sampled habitat	Number of m^2 samples	Woodland species	Grassland species	Arable species	Others*	Total
Woodland on limestone	51	65	23	1	5	94
Meadows	40	7	64	8	0	79
Cereal arable	55	5	38	69	2	114

* Includes species primarily associated with wetland or skeletal habitats (cliffs, walls and rock outcrops).

imental mixture was accurately predicted from independent measurements of shoot and root foraging by isolated plants growing in a standardized patchy environment. From this investigation it was concluded that dominance was achieved by the development of a coarse-grained architecture in which main roots and shoots spread rapidly through a large volume of habitat with rather imprecise concentration in resource-rich sectors. A complementary foraging mechanism was recognized in subordinates; here resource capture was achieved by a precise but local concentration of roots and shoots in resource-rich patches, a specialization likely to carry the penalty of subordination and ultimately (in circumstances of unrestricted growth and consolidation by the dominants) risk of competitive exclusion.

We may conclude, therefore, that functional diversity among dominants and perhaps also within subordinates is capable of immediate impacts on the properties of ecosystems. However, it may be a mistake to narrow the search for beneficial effects of biodiversity to an examination of immediate effects; the role of minor vegetation components may become evident only when viewed in the long term. The remainder of this paper outlines two hypothetical mechanisms whereby benefits of biodiversity may accrue from intermittent effects of minor contributors to the plant biomass. The first hypothesis involves subordinates, the second transients.

Filter effects of biodiversity; a role for subordinates?

So far in this paper it has been convenient to regard the plant community as a stable hierarchy containing dominants, subordinates and transients. In reality, of course, communities experience fluctuations in composition driven by seasonal and longer-term changes in climate, herbivory and vegetation management and by the intrinsic dynamics of component plant populations. Moreover, from field observations and experiments there is strong circumstantial evidence that the persistence of subordinates in both grassland and woodland vegetation is frequently dependent upon periodic events (e.g. droughts, frosts, floods, windthrows, grazing, trampling, burning, coppicing) that temporarily restrict the vigour and competitive effects of dominant plants. The literature contains many references to circumstances where abatement of such damaging events has led to expansions by dominants, losses of subordinates and a rapid decline in species richness (Tansley & Adamson 1925; Thomas 1960; Smith *et al.* 1971). There can be little doubt, therefore, that plant species that habitually dominate particular plant communities usually exert controlling effects on the fitness of their subordinates. However, since it is suspected that the immediate controls on ecosystem properties are largely determined by the dominants it is much more relevant to the purposes of this paper to

ask 'Do subordinate members of plant communities exercise controls on the identity, functional diversity and relative abundance of dominants?'

In order to review the opportunities for subordinates to control dominants it is necessary to consider the long-term dynamics of vegetation and the regenerative phases in the life cycles of dominants. From studies of vegetation succession (e.g. Watt 1925, 1947) it is established that continued dominance by particular species is frequently determined by the success of seedling or vegetative re-establishment following disturbance events causing mortalities of dominants on either a local or catastrophic scale. Here it may be important to recognize that often the early course of events following a disturbance is a temporary expansion in the cover and vigour of subordinates. This phenomenon is most obvious in forest clearings where a dense low cover of shrubs, herbs and bryophytes may provide the context for regenerating trees (Watt 1925; Skutch 1929; Marks 1974; Bormann & Likens 1979), but similar phenomena have been described for grasslands and heathlands (Oosting 1942; Keever 1950; Hillier 1990). Patterns of seedling and vegetative establishment following disturbances are not determined exclusively by regenerative traits such as the size and number of propagules and their dispersal, dormancy, morphology and physiology. They arise also through complex interactions with substratum conditions in which contributions to the ground cover by subordinate plants may be expected to have both positive and negative effects (Cavers & Harper 1967; Ross & Harper 1972; Grubb 1977; Connell & Slatyer 1977; Noble & Slatyer 1979; Pickett & White 1985; Bazzaz 1986; Maguire & Forman 1983; Burke & Grime 1996). Benefits to establishment have been described in circumstances where seedlings survive in the shelter afforded by low-growing shrubs, herbs and bryophytes (Lawrence & Hulbert 1960; Ward 1990; Hillier 1990). Negative effects of shrub, herbaceous and bryophyte cover on the establishment of grassland and forest dominants have been observed (Wardle 1959; Niering & Goodwin 1962; Webb *et al.* 1972; Pons 1989) and it is widely accepted (Fenner 1992) that many small-seeded herbs, trees and shrubs are incapable of establishment where there is a closed cover of vegetation. There is some evidence that quite inconspicuous subordinate members of the plant community can exert a selective effect on seedling populations of regenerating dominants. For example, in a microcosm experiment reported in Grime (1987) an algal film on the soil surface suppressed the development of small-seeded species but permitted establishment of larger-seeded grasses. The significance of subordinates in plant communities therefore may extend beyond any immediate contributions to the carbon economy and nutrient dynamics. Over the longer term there appears to be a potential for subordinate members of a plant community to act as a filter selecting between different potential dominants

during the early phases of recolonization following a disturbance event. Such selection could operate on the basis of variation in the seed reserves of dominants and the associated differences in the capacity of their seedlings to penetrate a low canopy (Grime & Jeffrey 1965; Westoby *et al.* 1992). Alternatively, according to the characteristics of the ground cover the filter might discriminate between dominants that rely upon rapid emergence and those which regenerate by persistent juveniles (Marshall 1927; Chippindale 1932; Marks 1974). Controlling effects of subordinates upon regenerating dominants may also occur through more indirect mechanisms, such as provision of sites in which seed predation is reduced (Thompson 1987; van Tooren 1988). In this review it has been considered prudent to restrict discussion of the possible filtering role of subordinates to rather direct effects on the recruitment of dominants. It would be possible, however, to include cases where the impact of subordinates arises from more complex phenomena such as the maintenance of critical pests, pathogens, herbivores or mutualists (e.g. Gilbert 1977; Huston & Gilbert 1996).

Evidence of a filter role for subordinates during ecosystem re-assembly remains anecdotal. There is an urgent need for carefully designed, long-term experiments (e.g. Ward 1990) to evaluate this phenomenon.

Founder effects of biodiversity; a role for transients?

On first inspection, transients appear to be irrelevant to ecosystem function. They occur as scattered individuals and many appear only briefly as seedlings that fail to survive. Familiar examples in European grasslands, for example, include annuals such as species of *Papaver* and *Polygonum* that occur as a legacy of former arable cultivations or seedlings of wind-blown or bird-dispersed herbs, shrubs and trees. Can such minor and incongruous constituents of vegetation affect the functioning and viability of ecosystems?

In order to explore the ecological significance of transients it is useful to identify the origin of these individuals and to consider why some communities contain a wider diversity than others. This review concentrates on the possible significance of transients as an indicator of the effectiveness with which potential dominants are dispersed across the landscape and recruited into 'suitable' ecosystems. However, it is also worth noting that transients represent a neglected subject in plant ecology and are worthy of studies beyond the scope of this review. In particular, there is a need to test the hypothesis that the accumulation and persistence of transients in species-rich vegetation is an indication that a low intensity of competition prevails in such conditions.

The sources of the transients appear to be seed banks in the soil and the seed rain from the sur-

rounding landscape. This suggests that the transients may provide useful information concerning the pool of potential colonizing species at each site. We may predict that a diversity of transients signifies the presence of a rich assortment of colonizers and a high probability that, in the event of habitat disturbance or changes in management, there will be a rapid ingress of different plant functional types, some of which may be capable of exploiting the new conditions. Here a specific example would be the benefit to woodland development where an abandoned grassland already contains a diverse assortment of tree seedlings.

Efforts to conserve biodiversity in Europe and in many other parts of the world takes place in a fragmenting landscape mosaic continuously disturbed by natural events and by urbanization, arable cultivation, forestry and various forms of grassland management. Successful conservation therefore depends in part upon continuous movement of populations and re-assembly of vegetation types and ecosystems. The extent to which communities and ecosystems are rapidly reconstituted is likely to be related to the reservoir of colonizers, many of which should be detectable prior to disturbance as transient constituents of the existing vegetation. Following Egler (1954) we may suspect that the speed and completeness with which ecosystem re-assembly occurs will depend upon early colonization by appropriate dominants and subordinates; late arrival may be expected to delay establishment of a species and may even exclude some completely (Keever 1950; Niering & Goodwin 1962; Holt 1972; Platt 1975). It follows, therefore, that the decline in diversity occurring in many contemporary landscapes is not simply a consequence of *in situ* losses within communities. Impoverishment may also occur through a progressive failure in the processes of plant dispersal and ecosystem re-assembly; this failure should be detectable as a decline through time in the density and species richness of transients in plant communities.

Implications for ecological theory

This paper has sought to connect recent studies of plant diversity and ecosystem function (e.g. Lawton 1994; Naeem *et al.* 1994; Tilman & Downing 1994) with another literature concerned with the mechanisms controlling diversity itself. Reference to investigations such as those of Whittaker (1975), McNaughton (1978) and Grime (1973) reveals that even in species-rich vegetation most of the plant biomass may reside in a small number of dominant species, the characteristics of which are likely to override as ecosystem controllers the effects of more numerous subordinate or transient components. As discussed by Huston (1997), this suggests a need for cautious assessment of studies (Naeem *et al.* 1994; Tilman & Downing 1994; Tilman *et al.* 1996; Tilman

et al. 1997) in which correlations are established between species richness and ecosystem properties but data are not presented with respect to the relative abundance of component species. Extreme care appears necessary where differences in species richness are not only correlated with differences in ecosystem functions but are also confounded with contrasting life histories and resource dynamics (e.g. Tilman & Downing 1994). However, until the results of long-term experiments measuring the functional characteristics of natural and synthesized ecosystems of contrasted species richness and functional composition are available, the possibility of immediate effects of species richness *per se* cannot be eliminated.

Even if the balance of evidence (Huston 1997; Grime 1997) continues to shift towards the mass ratio hypothesis and against the proposition that species richness controls the immediate functioning of ecosystems, this does not mean that losses of plant diversity should be viewed with equanimity. Declining diversity may be associated with less obvious impacts that operate through failures in filter and founder effects. In particular we suspect that there may be a progressive loss of functions in circumstances where vegetation patch dynamics and ecosystem reassembly continue against the background of a declining pool of colonizing propagules. According to this hypothesis the significance of plant diversity in relation to deterioration of ecosystem functions may arise primarily from its effects on the recruitment of dominants rather than any immediate effects of species richness *per se*.

Acknowledgements

References

Aarssen, L.W. (1997) High productivity in grassland ecosystems: effected by species diversity or productive species? *Oikos*, **80**, 183–184.

Al-Mufti, M.M., Sydes, C.L., Furness, S.B., Grime, J.P. & Band, S.R. (1977) A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *Journal of Ecology*, **65**, 759–791.

Armstrong, R.H. & Eadie, J. (1973) Lamb growth on grass and clover diets. *Proceedings of the British Society of Animal Production*, **2**, 68–74.

Barr, C.J., Bunce, R.G.H., Clarke, R.T., Fuller, R.M., Furse, M.T., Gillespie, M.K., Groom, G.B., Hallam, C.J., Hornung, M., Howard, D.C. & Ness, M.J. (1993)

Countryside Survey: *Main Report* 1990, *Department of the Environment*, *Vol.* 2. HMSO, London.

Bazzaz, F.A. (1986) Life history of colonising plants: some demographic, genetic and physiological features. *Ecology of Biological Invasions of North America and Hawaii* (eds H. A. Mooney & J. A. Drake), pp. 44–57. Springer Verlag, New York.

Bobbink, R. & Willems, J.H. (1987) Increasing dominance of *Brachypodium pinnatum* (L.) Beauv. in chalk grassland: a threat to a species-rich system. *Biological Conservation*, **40**, 301–314.

Bormann, F.H. & Likens, G.E. (1979) *Pattern and Process in a Forested Ecosystem*. Springer Verlag, Berlin.

Braun-Blanquet, J. (1932) *Plant Sociology: the Study of Plant Communities*. McGraw Hill, New York.

Bray, J.R. & Curtis, J.T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 325–349.

Burke, M.J.W. & Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology*, **77**, 776–790.

Campbell, B.D., Grime, J.P. & Mackey, J.M.L. (1991) A trade-off between scale and precision in resource foraging. *Oecologia*, **87**, 532–538.

Cavers, P.B. & Harper, J.L. (1967) Studies in the dynamics of plant populations. I. The fate of seed and transplants introduced into various habitats. *Journal of Ecology*, **55**, 59–71.

Chippindale, H.G. (1932) The operation of interspecific competition in causing delayed growth of grasses. *Annals of Applied Biology*, **19**, 221–242.

Clements, F.E. (1905) *Research Methods in Ecology*. University Publishing Company, Wisconsin.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. *American Naturalist*, **111**, 1119–1144.

Egler, F.E. (1954) Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio*, **4**, 412–417.

Fenner, M. (1992) *Seeds*: *the Ecology of Regeneration in Plant Communities*. CAB International, Wallingford.

Furness, S.B. & Grime, J.P. (1982) Growth rate and temperature responses in bryophytes. I. An investigation of *Brachythecium rutabulum*. *Journal of Ecology*, **70**, 513–523.

Gilbert, L. (1977) The role of insect–plant co-evolution in the organisation of ecosystems. *Comportement des insectes et milieu tropique* (ed. V. Labyrie), pp. 399–413. CNRS, Paris.

Grime, J.P. (1973) Control of species density in herbaceous vegetation. *Journal of Environmental Management*, **1**, 151–167.

Grime, J.P. (1987) Dominant and subordinate components of plant communities – implications for succession, stability and diversity. *Colonisation, Succession and Stability* (eds A. Gray, P. Edwards & M. Crawley), pp. 413–428. Blackwell, Oxford.

Grime, J.P. (1997) Biodiversity and ecosystem function: the debate deepens. *Science*, **277**, 1260–1261.

Grime, J.P. & Jeffrey, D.W. (1965) Seedling establishment in vertical gradient of sunlight. *Journal of Ecology*, **53**, 621–642.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology*: *a Functional Approach to Common British Species*. Unwin Hyman, London.

Grime, J.P., Shacklock, J.M.L. & Band, S.R. (1985) Nuclear DNA content, shoot phenology and species coexistence in a limestone grassland community. *New Phytologist*, **100**, 435–444.

Grubb, P.J. (1977) The maintenance of species-richness in

plant communities: the importance of the regeneration niche. *Biological Reviews*, **52**, 107–145.

Grubb, P.J., Kelly, D. & Mitchley, J. (1982) The control of relative abundance in communities of herbaceous plants. *The Plant Community as a Working Mechanism* (ed. E. Newman), British Ecological Society No. 1, pp. 77–97. Blackwells, Oxford.

Hillier, S.H.H. (1990) Gaps, seed banks and plant species diversity in calcareous grasslands. *Calcareous Grasslands: Ecology and Management* (eds S. H. H. Hillier, D. W. H. Walton & D. A. Wells), pp. 57–66. Bluntisham Books, Huntingdon.

Holt, B.R. (1972) Effect of arrival time on recruitment, mortality and reproduction in successional plant populations. *Ecology*, **53**, 668–673.

Hooper, D. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, **277**, 1302–1305.

Huston, M.A. (1997) Hidden treatments in ecological experiments: evaluating the ecosystem function of biodiversity. *Oecologia*, **110**, 449–460.

Huston, M.A. & Gilbert, L. (1996) Consumer diversity and secondary production. *Biodiversity and Ecosystem processes in Tropical Forests* (eds G. Orians, R. Dirzo & J. H. Cushman), pp. 33–47. Springer Verlag, Berlin.

Huston, M.A. & Smith, T.M. (1987) Plant succession: life history and competition. *American Naturalist*, **130**, 168–198.

Keever, C. (1950) Causes of succession on old fields of the Piedmont, North Carolina. *Ecological Monographs*, **20**, 229–250.

Kemp, P.R. & Williams, G.J. III (1980) A physiological basis for niche separation between *Agropyron smithii* (C$_3$) and *Bouteloua gracilis* (C$_4$). *Ecology*, **61**, 846–858.

Kent, M. & Coker, P. (1992) *Vegetation Description and Analysis: A Practical Approach*. Belhaven Press, London.

Lawrence, D.B. & Hulbert, L. (1960) Growth stimulation of adjacent plants by lupin and alder on recent glacier deposits in south-east Alaska. *Bulletin of the Ecological Society of America*, **31**, 58.

Lawton, J. (1994) What do species do in ecosystems? *Oikos*, **71**, 367–374.

LeCren, E.D., Kipling, C. & McCormack, J.C. (1972) Windermere: effects of exploitation and eutrophication on the salmonid community. *Journal of the Fishery Research Board of Canada*, **29**, 819–832.

MacGillivray, C.W., Grime, J.P. & the ISP Team (1995) Testing predictions of resistance and resilience of vegetation subjected to extreme events. *Functional Ecology*, **9**, 640–649.

McNaughton, S.J. (1978) Stability and diversity of ecological communities. *Nature*, **274**, 251–253.

Maguire, D.A. & Forman, R.T.R. (1983) Herb cover effects on tree seedling patterns in a mature hemlock-hardwood forest. *Ecology*, **64**, 1367–1380.

Marks, P.L. (1974) The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecological Monographs*, **44**, 73–88.

Marshall, R. (1927) The growth of hemlock before and after release from suppression. *Harvest Forest Bulletin*, **11**, 1–60.

Mellinger, M.V. & McNaughton, S.J. (1975) Structure and function of successional vascular plant communities in Central New York. *Ecological Monographs*, **45**, 161–182.

Mitchley, J. & Grubb, P.J. (1986) Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot-

and field-experiments on the role of interference. *Journal of Ecology*, **74**, 1139–1166.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. & Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature*, **368**, 734–737.

Niering, W.A. & Goodwin, R.H. (1962) Ecological studies in the Connecticut Arboretum Natural Area. I. Introduction and survey of vegetation types. *Ecology*, **43**, 41–54.

Noble, J.C. & Slatyer, R.O. (1979) The effect of disturbance on plant succession. *Proceedings of the Ecological Society of Australia*, **10**, 135–145.

Oosting, H.J. (1942) An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist*, **28**, 1–126.

Pastor, J. & Post, W.M. (1986) Influence of climate, soil moisture and succession on forest carbon and nitrogen cycles. *Biogeochemistry*, **2**, 3–27.

Pearson, T.H. & Rosenberg, R. (1976) A comparative study of the effects on the marine environment of wastes from cellulose industries in Scotland and Sweden. *Ambio*, **5**, 77–79.

Pickett, S.T.A. & White, P.S. (1985) *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando.

Platt, W.J. (1975) The colonisation and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs*, **45**, 285–305.

Pons, T.L. (1989) Dormancy, germination and mortality of seeds in heathland and inland sand dunes. *Acta Botanica Neerlandica*, **38**, 327–335.

Ratcliffe, D. (1961) Adaptation to habitat in a group of annual plants. *Journal of Ecology*, **49**, 187–203.

Ross, M.A. & Harper, J.L. (1972) Occupation of biological space during seedling establishment. *Journal of Ecology*, **60**, 77–88.

Sala, O.E., Lauenroth, W.K., McNaughton, S.J., Rusch, G. & Zhang, X. (1996) Biodiversity and ecosystem functioning in grasslands. *Functional Roles of Biodiversity; A Global Perspective* (eds H. A. Mooney, J. H. Cushman, F. Medina, O. E. Sala & E. D. Schulze), pp. 129–149. John Wiley and Sons, Chichester.

Shugart, H.H. (1984) *A Theory of Forest Dynamics*. Springer Verlag, New York.

Skutch, A.F. (1929) Early stages of plant succession following forest fire. *Ecology*, **10**, 177–190.

Smith, S.H. (1968) Species succession and fishery exploitation in the Great Lakes. *Journal of Fishery Research of the Board of Canada*, **25**, 667–693.

Smith, C.J., Elston, J. & Bunting, A.H. (1971) The effects of cutting and fertiliser treatments on the yield and botanical composition of chalk turf. *Journal of the British Grassland Society*, **26**, 213–223.

Spedding, C.R.W. & Diekmahns, E.C. (1972) *Grasses and Legumes in British Agriculture*. Commonwealth Agricultural Bureau, Farnham.

Tansley, A.G. & Adamson, R.S. (1925) Studies of the vegetation of the English chalk. III. The chalk grasslands of the Hampshire–Sussex border. *Journal of Ecology*, **13**, 177–223.

Thomas, A.S. (1960) Changes in vegetation since the advent of myxomatosis. *Journal of Ecology*, **48**, 287–306.

Thompson, K. (1987) Seeds and seed banks. *New Phytologist*, **106** (Suppl.), 23–34.

Tilman, D. & Downing, J.A. (1994) Biodiversity and stability in grasslands. *Nature*, **367**, 363–365.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, **277**, 1300–1302.

Tilman, D., Wedin, D. & Knops, J. (1996) Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, **379**, 718–720.

van Tooren, B.F. (1988) The fate of seeds after dispersal in chalk grasslands: the role of the bryophyte layer. *Oikos*, **53**, 41–48.

Vitousek, P.M. & Melillo, J.M. (1979) Nitrate losses from disturbed forests; patterns and mechanisms. *Forest Science*, **25**, 605–619.

Ward, L.K. (1990) Management of grassland–scrub mosaics. *Calcareous Grasslands*: *Ecology and Management* (eds S. H. Hillier, D. W. H. Walton & D. A. Wells), pp. 134–139. Bluntisham Books, Huntingdon.

Wardle, P. (1959) The regeneration of *Fraxinus excelsior* in woods with a field layer of *Mercurialis perennis*. *Journal of Ecology*, **47**, 483–497.

Wardle, D.A., Zackrisson, O., Hornberg, G. & Gallet, C. (1997) The influence of island area on ecosystem properties. *Science*, **277**, 1296–1299.

Watt, A.S. (1925) On the ecology of the British beechwoods with special reference to their regeneration. Part II, Sections II and III. The development and structure of beech communities on the Sussex Downs. *Journal of Ecology*, **13**, 27–73.

Watt, A.S. (1947) Pattern and process in the plant community. *Journal of Ecology*, **35**, 1–22.

Webb, L.J., Tracey, J.G. & Williams, W.T. (1972) Regeneration and pattern in the sub tropical rain forest. *Journal of Ecology*, **60**, 675–695.

Westoby, M.E., Jurado, E. & Leishman, M. (1992) Comparative evolutionary ecology of seed size. *Trends in Ecology and Evolution*, **7**, 368–372.

Whittaker, R.H. (1965) Dominance and diversity in land plant communities. *Science*, **147**, 250–260.

Whittaker, R.H. (1975) *Communities and Ecosystems*, 2nd edn. Macmillan, New York.

Willis, A.J. (1963) Braunton Burrows: the effects on the vegetation of the addition of mineral nutrients to the dune soils. *Journal of Ecology*, **51**, 353–374.