

## Restoration of Biodiversity and Ecosystem

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### ABSTRACT

Succession is one of the most studied processes in ecology and succession theory provides strong predictability. However, few attempts have been made to influence the course of succession thereby testing the hypothesis that the passage of one stage is essential to enter a next one. At each stage of succession ecosystem processes may be affected by the diversity of species present, but there is little empirical evidence showing that plant species diversity may affect succession. The main objective in the present study is to test if there is any effect of plant species diversity on the functioning of artificially-created grassland communities. We were mostly interested in how successful is the sowing of meadow species into newly abandoned land and how long do the effect of initial sowing persist, how is affected the set of natural colonizers, which includes both the weed species and also the later successional species arriving naturally into the zone. One of the main questions concerning succession is to which extent the trajectory may be predictable or not. What will be the consequence of the different succession pathways for ecosystem processes, such as productivity and resource utilization, as well as species composition of both above and belowground communities? What will be the subsequent effects of feed back to vegetation development through initial manipulation of vegetation after land abandonment? And, finally, how general may results be when obtained in specific conditions? Our hypothesis is that an increase in the initial plant species diversity at the start of secondary succession enhances the amount of biomass produced and consequently stimulates the soil microbial biomass and the abundance of soil invertebrates. It has been suggested that changes in plant species diversity affect several ecosystem processes, such as primary productivity, nutrient retention and vegetation dynamics. A positive impact of species diversity on plant productivity has been explained by the complementarity of resource use among plant species or their functional groups.

**Keywords:** Biodiversity, Changed Land Use, Complementary Resource Use, Community Assembly, Ecosystem Processes, Plant Functional Groups, Sampling Effect, Secondary Succession, Species Richness, Stability

## 1. INTRODUCTION

### 1.1. Land Use Change

Due the intensification of agricultural practices and developments, European Union has introduced set-aside measures for agricultural land. When agricultural land is

set aside permanently, restoration of natural ecosystems may be achieved in which the ecosystem has maximum carrying capacity in terms of biodiversity, biomass and nutrient cycling. This process has been frequently studied, becoming a model for community ecological studies (Orians *et al.*, 1996). Since the dynamics of secondary succession are much faster than those of

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primary succession, it has enabled experimental testing of various theories on dispersal, colonization and establishment (Armesto and Pickett, 1986). Therefore, studying old field succession has both fundamental and applied value. However, the predictability of old field succession and of the effects of various management strategies still needs improvement (Leps *et al.*, 2007).

In the debate of threats to biological diversity and ecosystem functioning, land use change has been identified as one of the most immediate causes (Vitousek *et al.*, 1997; Sala *et al.*, 2000). Diversity losses in plant communities can limit plant recruitment and decrease plant productivity, which will pose transient effects on the ecosystem functioning (Symstad and Tilman, 2001). There is a growing awareness of how agricultural practices decrease diversity, not only of plants but also of soil micro-organisms (Helgason *et al.*, 1998). Today, substantial effort is made to restore diversity of former arable land. Indeed, management modifying the initial plant community increases the rate of transfer towards more natural grasslands or forest communities (Hansson and Fogelfors, 1998; Putten *et al.*, 2000).

Humans are altering the composition of biological communities through a variety of activities that increase rates of species invasions and species extinctions, at all scales, from local to global. These changes in components of the Earth's biodiversity cause concern for ethical and aesthetic reasons, but they also have a strong potential to alter ecosystem properties and the goods and services they provide to humanity. Ecological experiments, observations and theoretical developments show that ecosystem properties depend greatly on biodiversity in terms of the functional characteristics of organisms present in the ecosystem and the distribution and abundance of those organisms over space and time. Species effects act in concert with the effects of climate, resource availability and disturbance regimes in influencing ecosystem properties (Hooper *et al.*, 2005). The scientific community has come to a broad consensus on many aspects of the relationship between biodiversity and ecosystem functioning, including many points relevant to management of ecosystems. Further progress will require integration of knowledge about biotic and abiotic controls on ecosystem properties, how ecological communities are structured and the forces driving species extinctions and invasions (Hooper *et al.*, 2005).

One of the widely applied measures to counteract the rapid loss of species diversity and to conserve the remaining diversity, is to convert former agricultural land into more natural ecosystems. Due to the long-term influence of cultivation, vegetation development on

abandoned arable land is known to be constrained by high soil fertility, disrupted fungal networks (Schulze and Mooney, 1993), depleted seed banks and limited propagule dispersal (Bakker and Berendse, 1999).

Growing awareness of the rapid loss of global biodiversity has stimulated the discussion on the functional relationship between species diversity and ecosystem processes (Schulze and Mooney, 1993; Heywood, 1996). At local and regional scales, land use changes are among the most immediate drivers of species diversity. Intensification of land use, especially the conversion of natural ecosystems into agro-ecosystems is supposed to both change the composition and reduce the diversity of biological communities (Putten *et al.*, 2000; Leps *et al.*, 2001). Therefore, one of the possibilities to counteract the current loss of biodiversity may be to reduce the intensity of land use (in the case of grassland), as well as to abandon cultivated land (in case of arable land).

## 1.2. Biodiversity Versus Secondary Succession

Vegetation development on permanently abandoned arable land (also known as old field succession) has acted as a model for many ecological studies on succession (Olf *et al.*, 1997). Changes in plant composition over time depend on the availability of propagules (Cooper and Power, 1997; Thompson and Starzomski, 2007), changes in soil fertility (Marrs, 1993), above- and belowground herbivore activity (Olf and Ritchie, 1998), the presence or absence of mutualistic symbionts (Clay and Holah, 1999) as well as feed-backs between plant species and their associated soil communities (Bever *et al.*, 1997; Westover *et al.*, 1997; Hedlund *et al.*, 2003). The final outcome of all these interactions determines which species may, at a certain stage of succession, successfully compete for the available resources. Sowing later succession species essentially changed the initial stage of vegetation development at abandoned arable land (Hansson and Hagelfors, 1998). As weed suppression depended on the number of species in the sown stands, the diversity of plant species at a certain stage may affect the course of succession at least temporary.

The first plant species to become established on abandoned arable land are weedy species that are already present in the seed bank (Cooper and Power, 1997). These are opportunists with relatively poor root exploitation capacity (Grime, 1997). During the initial stage of land abandonment the initially colonising plant species are replaced by persistent perennials (Hansson and Hagelfors, 1998; Kosola and Gross, 1999). If plant propagules reach abandoned arable land by the time the vegetation is dominated by persistent

perennials, poor establishment conditions can be crucial constraints of succession to species rich vegetation.

Ongoing long-term studies show that the development of a species-rich vegetation on abandoned arable land is often constrained even when natural abiotic conditions have been restored (Bakker and Berendse, 1999). One of the main reasons is that the seed bank has been depleted (Cooper and Power, 1997) and that many late-succession species have poor seed (or propagule) dispersal (Bakker and Berendse, 1999). Another constraint, which has received less attention, is that persistent competitive weed species may prevent vegetation development for many years (Leps and Rejmanek; 1991; Hansson and Hagelfors, 1998).

Experimental manipulations can confound the effect of species identity with the effects of diversity per se (Huston, 1997). Some species are often better at “doing the job” than others. So experiments need to be designed carefully to avoid the possibility that the effect of a particular species is mistakenly interpreted as an effect of diversity. The best solution should be an experimental design in which the low diversity treatments are composed of various subsets of species in the high diversity treatment, designed in such a way that each species is equally important at all the diversity levels examined. In addition, some species are more similar to each other than to other species, leading to the concept of functional groups. For example, two narrow-leaved grasses are functionally more similar to each other than a grass and a forb. Consequently, the diversity effect (if any) has a hierarchical nature (e.g., the diversity of functional groups, species diversity within functional groups).

During the course of secondary succession there is a change in species number as well in productivity. In general plant diversity decreases while productivity increases (Mooney and Godron, 1983). These trends are founding in several studies (Montalvo *et al.*, 1993). The typical sequence of many secondary successions in temperate regions is the rapid transition from an annual herb-dominated plant community to a perennial herb and grass community before shrub and tree establishment begins (Gray *et al.*, 1987). The same authors recognize four types of plant community, though the relative timing of these communities will vary from succession to succession: Ruderal, typically the first year of succession when the annuals dominate; early-successional, the second to fifth year where annual and biennial herbs are declining but perennials and grasses are stabilising; mid-successional, from the fifth to fifteenth year when grasses and perennials

dominated although tree and shrub establishment is beginning; late successional, when the latter are dominant.

Based on this and previous studies, species richness effects, when objectively demonstrated, may only arise within a narrow range of functional composition (e.g., mid-successional grassland species such as those used in communities assembled at Cedar Creek (Tilman, 1999) or in the BIODDEPTH project (Hector *et al.*, 1999). Effects measured may then be due to a combination of species identity or trait effects (Symstad *et al.*, 1998) and true complementarity (Hooper and Vitousek, 1997), for example, because of including nitrogen fixing plant species. On the other hand, as soon as functionally different species are mixed, for example species from different succession stages, the effects of differences in traits override any species richness effects and the relative abundance of different functional groups becomes the meaningful metric to characterise diversity effects (Nijs and Roy, 2000).

The manipulations of the succession assay consist in the introduction of later successional plant species, mainly perennial species. As a consequence of this manipulation the course of succession have been affected due the change in the dominance pattern in vegetation (Diaz and Cabido, 2001). From a study concerning the first four years of the succession concluded the floristic composition changed more rapidly than the performance of the dominant species. The effect of the sown diversity treatments was the rearrangement of most seasonally variable community (Gray *et al.*, 1987) of early-successional species by weed suppression to a community when grasses and perennials dominated.

Local species assemblages reflect the interaction of processes acting on local (e.g., competition, predation, disturbance) and regional (e.g., long-distance dispersal, speciation, habitat history) scales. This interaction may be reflected by the relationship between local ( $S_L$ ) and regional species richness ( $S_R$ ) for a set of like communities (Loreau, 2000). It is often presumed that communities that can accommodate additional local species with increasing regional richness are ‘unsaturated’ and feature significant linear trends in  $S_L$ – $S_R$  plots. By contrast, communities unable to accommodate addition local species are deemed “saturated” and result in either decelerating curvilinear trends or insignificant increases in  $S_L$  with increasing  $S_R$  (Szava-Kovats *et al.*, 2012).

The temporal variability of ecological communities may depend on species richness and composition due to a variety of statistical and ecological mechanisms. However, ecologists currently lack a general, unified theoretical framework within which to compare the

effects of these mechanisms. Developing such a framework is difficult because community variability depends not just on how species vary, but also how they covary, making it unclear how to isolate the contributions of individual species to community variability (Fox, 2010). The effects of species loss on community variability can be partitioned into effects of species richness (random loss of species), effects of species composition (non-random loss of species with respect to their variances and covariances) and effects of context dependence (post-loss changes in species' variances and covariances).

All ecological systems fluctuate over time. Understanding the causes and consequences of this temporal variability is a fundamental goal of ecology. At the community level, variability can be measured as fluctuations in the total biomass or abundance of all species, or in an assemblage of similar species (Cottingham *et al.*, 2001). Community variability is of fundamental interest as an index of community stability (Steiner *et al.*, 2005) and of applied interest as an indicator of ecosystem stress and the near-term potential for regime shifts.

Theoretical models identify mechanisms linking community variability to species richness and numerous empirical studies have tested for these mechanisms (Ruijven and Berendse, 2007). But ecologists currently lack a unified framework within which to compare these mechanisms. Studies of community variability also have lacked a way to distinguish effects of species richness from effects of species composition. Separating the effects of species richness from those of species composition has been a central concern in studies of biodiversity and ecosystem function (Hooper *et al.*, 2005; Fox, 2010). Community variability is an ecosystem function in the sense that it is a collective property of the species comprising the community. However, studies of community variability have focused on effects of species richness, not species composition (Lehman and Tilman, 2000; Cottingham *et al.*, 2001). Some experimental studies of community variability have statistically separated effects of species richness and composition (Steiner *et al.*, 2005). However, because the required experimental designs often are impractical, there is a need for a way to partition the effects of species richness and composition on community variability in a broader range of settings.

Many areas of ecology are concerned with relational properties of species. Community ecology considers how the niche differentiation of species from one another

changes as species immigrate, go extinct and shift their niches (Scheffer and Nes, 2006; Fox and Vasseur, 2008). Many studies of biodiversity and ecosystem function ask whether individual species make 'redundant' contributions to ecosystem function or unique, irreplaceable contributions (Wohl *et al.*, 2004).

Another newly-identified effect of species loss on community variability arises in the context of mean-variance scaling: mean-variance scaling interacts with any process or factor that alters the slope and intercept of the mean-variance relationship. Previous studies of mean-variance scaling, including those that test for context dependence of the mean-variance scaling relationship, have not recognized this interaction term (Tilman *et al.*, 1998; Tilman, 1999; Cottingham *et al.*, 2001; Petchey *et al.*, 2002; Valone and Hoffman, 2002; Leps, 2004; Steiner, 2005; Steiner *et al.*, 2005).

### 1.3. Species Richness

The species composition of natural communities is a result of competitive forces acting over time. The species that are present are there because they were able to survive in the competitive struggle, potentially the result of niche complementarity. It is not clear whether diversity will have the same effect in randomly assembled mixtures of species, such as those used in manipulative experiments, as in a community in which species composition has developed and stabilised over a long period.

The species richness of arable field seed bank is often high. It has been shown many times that the initial species richness of newly abandoned field could be very high, but the species richness drops due to spreading of competitively strong species and competitive exclusion of subordinate species (Leps *et al.*, 2007). Although some arable weed species are considered rare and endangered, their survival is usually dependent on regular ploughing and they are not able to survive in permanent grassland, particularly under mesic or wet conditions. Also, many competitively strong weeds are undesirable in the communities.

The development of the community is often affected by the presence of strong dominants. This part of the course of the community development is highly idiosyncratic, as it depends on the local conditions and on the presence of a species able under given condition attain high dominance (Leps *et al.*, 2007).

During grassland secondary succession, species richness tends to decrease with time as a result of increased dominance by productive species (Huston,

1994; Bazzaz, 1996). At our sites, increased dominance by perennials led indeed to a decrease in total species richness, with the loss of subordinate annuals. Thus, the negative correlation found for the Dutch and Swedish sites between aboveground biomass and species richness was a secondary effect of successional development rather than a direct effect of species richness per se.

#### 1.4. Productivity-Diversity Relationship

The biomass pattern cannot be explained by the hypothesis that more diverse plant communities are more productive (Schulze and Mooney, 1993). The change in the number of species present or species richness per se had no effect on biomass or when appear it was negative relationships. In most cases the pattern can be explained as a function of the specific characteristics of the species present, independently of the functional group. The specific characteristics including soil fertility and climatic parameters (Sala *et al.*, 1988; Lane *et al.*, 1998), determined different absolute values for biomass production and rate of successional development.

When considering total plant species richness, the observed patterns were in disagreement with the hypothesis that increased productivity results from higher species diversity in grasslands (Tilman *et al.*, 1996; Hector *et al.*, 1999). This lack of a clear relationship between species richness and biomass production in a experimental grasslands (Leps *et al.*, 2001) was also demonstrated by the lack of consistent differences between plots sown with low or high numbers of grassland species. The variance in the species composition between the different replicates of the Low diversity plots, as a consequence of their lower diversity, resulted in highly variable productivity. Diaz and Cabido (2001) show that patterns of productivity where primarily the result of the degree of dominance of grassland perennials over annual arable weeds. This finding validated the hypothesis that the response of ecosystem functioning to changing diversity relates more to species traits than to species numbers per se (Chapin *et al.*, 2000).

As in a negative productivity-diversity relation, also the biomass of forb group was influenced negatively by the richness species in the plots, showing that the functional diversity had also an effect on productivity and the efficiency of capture of resources (Jiang *et al.*, 2007). Similar pattern was established by Guo *et al.* (2006), being the first author explaining the negative productivity-diversity relation. The decrease of species richness, the effective diversity of Shannon index  $e^H$  or

the Camargo theory not showed any significant relation with the productivity. Several authors indicated a positive effect of diversity on productivity due to niche complementarity (Tilman *et al.*, 1996; Hector, 1998; Loreau, 1998; Loreau *et al.*, 2001; Wardle and Zackrisson, 2005; Grace *et al.*, 2007). Diaz and Cabido (2001) showed that plots sown with a high diversity mix of grassland species had higher biomass, both above- and belowground and therefore in total and that these plots were more efficient in capturing light and using photosynthetic products, than plots left to natural successional dynamics after land abandonment.

Changes in plant community composition independent of diversity can have similar significant effects on biomass. Decreasing the diversity of an assemblage by just one species can have a positive, negative, or negligible effect on either plant biomass, depending on the identity of the species lost and, in some cases, the composition of the community from which it was lost. The functional group to which a species belongs seems to be a good predictor for the type of the impact a species has on biomass.

One anomaly is why there appears to be no increase in productivity whit the addition of new species within a grow form, if it is assumed that new species enter by exploiting a new or expanded resources base. There are three possible explanations for this: (1) new species do increase productivity, but the increment cannot be detected given the high variability of productivity measurements in natural system; (2) the resource base is expanded by newly entering species, but the cost of additional non-photosynthetic components (root, stem, or storage tissue) needed to mine these resources offsets the potential gain in productivity; (3) new species do not expand the resources base, but simply displace existing species.

The model of Tilman *et al.* (1997) assumes that all plant communities eventually become monocultures, so the question arises whether the productivity of systems that never become monocultures is also related to their diversity? Contrary to Tilman *et al.* (1997), the model by Loreau (1998) does not compel species assemblages to become monospecific. This model describes the fluxes of a limiting inorganic nutrient in plants, detritus, the local depletion zones around the roots and in the shared, regional pool of inorganic nutrients. Community biomass is calculated from the nutrient uptake by each species from its local depletion zone and the concentrations in these zones are obtained by balancing the inflows and outflows in all compartments of the system at

equilibrium. To introduce differences in species traits, Loreau (1998) varies the average resource.

If the species occupy similar resource depletion zones, the consequences of these contrasting scenarios for community biomass are opposite. Alternatively, if the species are highly complementary (occupying different resource depletion zones), a higher species number always enhances community biomass. Reality may lie between the extremes of zero and complete resource complementarity, so diversity-productivity curves can be expected to take different forms. The question remains whether, in general, addition of species increases or decreases the average resource use intensity. The sampling effect suggests that the first possibility is most likely. However, it has not been examined in great detail how the sampling effect operates, nor whether the mechanism can be generalised.

Moreover, until now, models as well as experiments have dealt mainly with species numbers and have given little attention to the influence of other components of diversity, for example species evenness (Rusch and Oosterheld, 1997). Also, the influence of having either small or large differences between the species of a community has remained basically unexplored, apart from manipulations of functional groups which address this indirectly (Hooper and Vitousek, 1997; Tilman *et al.*, 1997). Diaz and Cabido (2001) have developed a model that partitions plant diversity into all these components: Species richness, species evenness and the degree of interspecific difference. The model is based on the capacities of individual plants to absorb nutrients and to convert them into biomass during exponential growth and differences in these capacities between species are allowed to operate through time during exponential growth, in the absence of interspecific interactions. Interspecific dissimilarity thus progressively changes the characteristics of the community as it develops. As a result, the influence of a higher probability to contain the fast-growing species in more diverse systems (the sampling effect) becomes analytically traceable.

Possible differences in productivity between sown diversity plots could be attributed to the respective capacity of the treatments to modify the relative proportion of the component species. Thus, biomass increased with increasing dominance of perennials in the community as a consequence of sowing and successional process (Putten *et al.*, 2000; Leps *et al.*, 2001). In this respect, the intermediate position and variable values of the low sown diversity plots (where different species combinations were sown while keeping constant the

number of species) between the values for natural colonisation and high sown diversity, discover the role of the species identity on manipulation of the succession process, independently of species diversity, this taken as the number of species (Tilman *et al.*, 1997; Hector, 1998). The variable productivity of low sown diversity plots can be explained because these communities are usually formed of species that differ in its capacity as strong dominants (Leps *et al.*, 2001). Similar conclusions were found by Naeem *et al.* (1996), where species poor-assemblages had wider ranges of possible productivities than more diverse assemblages and Symstad *et al.* (1998) in which experiment demonstrated the variance in individual species effects on productivity, founding that this effect appears to be most important at very low levels of diversity.

Different patterns are shown from data obtained regarding analysis of productivity by functional groups. Thus, the initial manipulation modified the relative importance of each functional group in the succession process, the leguminous and forb components being incorporated in the manipulated plots (Leps *et al.*, 2001). Wardle *et al.* (1999) suggest that enriched functional groups richness is likely to enhance productivity through complementary effects of coexisting species with partially non-overlapping niches. Nijs and Roy (2000) assume that functional group diversity determined productivity more strongly than species diversity and Tilman *et al.* (1997) and Hector *et al.* (1999) found a positive relationship between the number of functional groups and above ground biomass. In both experiments, it was the functional composition (i.e., the identity of the functional group present) which had the larger impact.

The increase in productivity is often the result of the introduction of a new life form, such as a shrub or a perennial herbs, this new growth form is able to tap an unutilized nutrient or resources of the habitat by virtue of its special traits (e.g., deeper roots) suggesting that species identity plays a large role than species number (Smith *et al.*, 1997). In addition, the dominance depends not merely upon resource acquisition but upon the way in which captured resources are utilized by plant; so the construction of a matrix of robust vegetative tissues allow to perennials the occupation of a site over an extended period (Grime, 1997). Species traits that alter the resource supply have just as strong effect on community processes because the balance of supply resources determine the competitive balance among species in the community (Tilman, 1990). In this way: Competitive exclusion is one of the mechanisms (Grime, 1997) that may operate during secondary succession and

probably causes the local extinction and rarefaction of some species (Al-Mufti *et al.*, 1977).

Early-successional species generally leading to a lower biomass and higher ratio of production to biomass (Shaver, 1995) and confirm the lower values reached in the natural colonization if compared with the sowing plots. The proportional increase in grasses and perennials in the aboveground biomass during secondary succession (Montalvo, 1992) have been found in several experiments (Huenneke and Mooney, 1989; Hansson and Hagelfors, 1998; Kosola and Gross, 1999) and are characteristic of the transit to mid-successional stage.

In a classic study on old field succession Odum (1960) found species number changed from five initial dominant annual and perennial herbs to a community of nearly 20 dominants in which one perennial genera contributed the greatest biomass. Odum found in the perennial herbs stage, species number increased but net productivity did not. The increase in productivity is often the result of the introduction of a new life form, such as a shrub or a perennial herbs, this new growth form is able to tap an unutilized nutrient or resources of the habitat by virtue of its special traits (e.g., deeper roots) suggesting that species identity plays a large role than species number (Smith *et al.*, 1997). In addition, the dominance depends not merely upon resource acquisition but upon the way in which captured resources are utilized by plant; so the construction of a matrix of robust vegetative tissues allow to perennials the occupation of a site over an extended period (Grime, 1997). Species traits that alter the resource supply have just as strong effect on community processes because the balance of supply resources determine the competitive balance among species in the community (Tilman, 1990). In this way: Competitive exclusion is one of the mechanisms (Grime, 1997) that may operate during secondary succession and probably causes the local extinction and rarefaction of some species (Al-Mufti *et al.*, 1977).

Functional group diversity determined productivity more strongly than species diversity (Nijs and Roy, 2000), if we may assume that species differ more widely between than within functional groups. In the past, functional groups have been delimited both by their response to perturbation or on the basis that they use the same resource (Smith *et al.*, 1997) and neither of these per se coincides with a classification according to productivity. Redefining functional groups with respect to their impact on ecosystem processes, as in Chapin *et al.* (1996), therefore seems useful.

The successful of perennial species is associated with the decreased in species richness in circumstances

where this is attributable to changes in the number of subordinates and transients and may explain the negative relationships established between richness and aboveground biomass. There are subordinate plants, which through a variety of mechanisms coexist with dominant plants. Grime (1998) suspect that the associations between certain dominants and their subordinates reflect a complementary exploitation of habitat resulting in a more complete capture of resources and minor benefits to productivity. In the other hand, more species do increase productivity, but the increment cannot be detected given the high variability of productivity measurements in natural system (Mooney and Godron, 1983).

The functional groups differ in both phenology and rooting depth implying a complementary exploitation of habitat, competitive interactions in mixture may have a strong effect on total plant biomass. In this way, Leps *et al.* (2001) shown a higher productivity when perennials are dominants; as consequence of the strong dominance, a lower richness results in the more productive plots. This negative diversity-productivity relationship can be explained by the competitive interactions between annual-perennial life forms beyond of complementarity. Evidence of complementary and/or positive interactions effect between species occurred and that the sampling effect was not the only mechanism at play (Tilman *et al.*, 1997; Hector *et al.*, 1999). In fact, the sampling effect and resource complementary, either in time or in space, may operate simultaneously (Hooper, 1998).

### 1.5. Nutrient Availability and Species Richness

Biodiversity is declining worldwide, with direct consequences for ecosystem functioning and services (Loreau *et al.*, 2001; Hooper *et al.*, 2005). Next to habitat loss and fragmentation, degradation of habitat quality is a major driver of biodiversity loss. Nutrient enrichment often causes a rapid decline of plant diversity (Crawley *et al.*, 2005) resulting in a strongly impoverished community.

This relationship between nutrient availability and species richness is described in two well-known views (Wilson and Tilman, 1993; Grime, 2001). The first view proposes that nutrient enrichment causes a shift in competition between plants for soil resources in low productive habitats to increased aboveground competition for light in high productive habitats (Tilman, 1988; Wilson and Tilman, 1993). The second view proposes that both above- and belowground competition increase with increasing soil fertility. In both cases species are outcompeted by strong competitors (Pierik *et al.*, 2011).

A consequence of such a selection for plant traits is that new species with traits suitable for nutrient-rich conditions are expected to colonize the fertilized communities. Clearly, these species should be present in the local or regional species pool with sufficient dispersal possibilities (Turnbull *et al.*, 2000; Hautier *et al.*, 2009). This could lead to a partial or even complete recovery of species richness. These plant communities would, however, exist of different species that exhibit a different set of plant traits. In addition, this mechanism predicts a lag time in species richness recovery because colonization processes take time.

### 1.6. Sampling and Complementary Effect

Sampling effects may be to the result of the enhanced chance of including species with a specific trait (e.g., high productivity) in species-rich compared to species-poor plant mixtures (Huston, 1997). Sampling effects are demonstrated by varying the plant species composition of low diversity treatments (Putten *et al.*, 2000). A positive impact of species diversity on, for example, primary productivity, may be the result of resource-use complementarity allowing more diverse communities to utilise a larger proportion of the ecosystem resources (Loreau, 1998). In order to establish whether such overyielding occurs in mixtures of plant species, information on the productivity of the monocultures of all individual plant species needs to be included in the comparison (Huston *et al.*, 2000). Using the performance of individual plant species in high diversity mixtures, their performance in low diversity mixtures may be predicted, but this is not sufficient to separate the sampling effect and from that of resource-use complementarity (Leps *et al.*, 2001).

The complementarity effect results from interspecific differences in resource partitioning. This can be the case when species compete for more than a single limiting resource and each of the species is better in exploitation of one or other of the resources, or each of them has a different response curve to some environmental factor which varies over space or time. In this case, high diversity mixtures should be more efficient at resource capture than the best of the monocultures or low diversity mixtures (Leps *et al.*, 2001).

On average, the performances (productivity, ability to suppress the weed species) of high diversity mixtures were usually better than those of the low diversity mixtures (Leps *et al.*, 2001). However the performance of the best low diversity mixture was usually as good as the best of the high diversity replicates. On the contrary, the worst performing low diversity mixture always produced less biomass and had poorer weed

suppression than the worst performing high diversity plot (Leps *et al.*, 2001). All these results suggest that this diversity effect was the result of the “chance effect”, i.e., with a higher number of species, the chance that influential species are present is higher. If there was some complementarity, than it was impossible distinguish it from the chance effect (Hector, 1998). The results correspond to the outcome of the “competition for one resource” model of Tilman *et al.* (1997), which is based completely on the “chance effect”. Similar results have also been obtained in other experiments (Naeem *et al.*, 1995).

Although empirical and theoretical studies suggest that community diversity, composition and invasibility may ultimately be mediated by the interplay between the effects of a spatially and temporally heterogeneous environment and the density and richness of the seeded species pool (Clark *et al.*, 2007; Questad and Foster, 2008; Myers and Harms, 2009), most seed-addition experiments are conducted at single locations and/or in single years (Wilsey and Polley, 2004; Clark *et al.*, 2007) and often lack simultaneous manipulations of seed density, seeded species richness, or disturbance (Clark *et al.*, 2007; Myers and Harms, 2009).

### 1.7. Biodiversity-Ecosystem Processes

Plant species differ in their ability to grow under different physical/chemical conditions that vary spatially, competing for a several resources at any given spatial location. The most widely cited mechanisms for increased competitive exclusion at high productivities are based on the idea that higher productivities will reduce spatial heterogeneity in the relative supplies of different resources, that reducing the number of species able to coexist. Tilman (1982) introduce a model based on the assumption that the two essential resources are mineral nutrients and light. A number of rather short-term experiments (Putten *et al.*, 2000; Leps *et al.*, 2001; Hedlund *et al.*, 2003) have indicated that, on average, species-rich mixtures are more productive and also more effective in suppression of weed species and preventing further colonization than species-poor mixtures (Putten *et al.*, 2000; Naeem *et al.*, 2000; Bullock *et al.*, 2001), with some low diversity mixtures being as productive and as effective as the high diversity mixtures; those successful low diversity mixtures are usually composed of species dominating the high diversity mixtures (Leps *et al.*, 2001).

Removal of plant functional groups, representing permanent exclusion of plant species from the species pool, has important consequences for ecosystem-level processes and properties such as primary production, biomass, decomposer activity, nutrient levels and

ecosystem stability, especially if species have separate niches and demonstrate complementary resource use. When niche overlap is high and competition for resources is intense, loss of a given species can be largely compensated for by the other species, resulting in overall biomass and productivity being less sensitive to species removal (Hooper, 1998).

Many functional characteristics of ecosystems are in some way connected to productivity and, because of the strong effect of productivity on diversity (Al-Mufti *et al.*, 1977), it is extremely difficult to interpret correlations between diversity and the functioning of ecosystems. For example, early- and late-successional communities differ not only in their stability characteristics and also in their species richness. Nevertheless, both differences are dependent on composition of prevailing life-history strategies in a community (Leps *et al.*, 2001).

Several empirical studies (Grime, 1997; Leps *et al.*, 2001) have demonstrated that ecosystem function is mainly a consequence of the prevailing strategies of constituent species, in interaction with the abiotic environment. Even some of the experimental effects that are ascribed to diversity are probably a consequence of the effect of abiotic conditions and species ecophysiology (Huston, 1997). However, the fact that species life histories are more important than diversity per se does not mean that diversity has no effect on ecosystem function. Indeed, the majority of ecologists are convinced about the importance of diversity for ecosystem processes (Schlapfer *et al.*, 1999).

In the debate of threats to biological diversity and ecosystem functioning, land use change has been identified as one of the most immediate causes (Vitousek *et al.*, 1997; Sala *et al.*, 2000). Diversity losses in plant communities can limit plant recruitment and decrease plant productivity, which will pose transient effects on the ecosystem functioning (Symstad and Tilman, 2001). There is a growing awareness of how agricultural practices decrease diversity, not only of plants but also of soil microorganisms (Brussard *et al.*, 1996; Helgason *et al.*, 1998; Read, 1998). Today, substantial effort is made to restore diversity of former arable land. Indeed, management modifying the initial plant community increases the rate of transfer towards more natural grasslands or forest communities (Hansson and Fogelfors 1998; Putten *et al.*, 2000). Different management regimes of grasslands are known to alter the biomass of soil fauna and to change the composition of microbial communities (Bardgett *et al.*, 1996; Bardgett and Cook, 1998; Donnison *et al.*, 2000; Hedlund, 2002). However, effects of restoring diversity of plant

communities on the composition of soil communities have received far less attention.

It has been suggested that changes in plant species diversity affect several ecosystem processes, such as primary productivity, nutrient retention and vegetation dynamics (Schlapfer and Schmid, 1999; Tilman, 1999; Chapin *et al.*, 2000; Loreau *et al.*, 2001). Experimental data indeed show a positive effect of the number of species on primary productivity and nutrient retention (Naeem *et al.*, 1994; Tilman *et al.*, 1996; 1997; Hooper, 1998; Hector *et al.*, 1999), but sampling effects may complicate the distinction between the effects of species traits and those of species diversity (Huston, 1997; Tilman *et al.*, 1998). A positive impact of species diversity on plant productivity has been explained by the complementarity of resource use among plant species or their functional groups (Diaz and Cabido, 2001; Loreau and Hector, 2001; Tilman *et al.*, 2001). Alternatively, it has been argued that an increase in plant diversity will increase the probability of including highly productive species into the plant community (Huston, 1997; Leps *et al.*, 2001).

A major challenge in ecology is to identify drivers of community composition and to disentangle their relative contribution in order to predict how species and communities change in response to alterations in their environment. For plant communities, traditionally the abiotic soil environment has been considered to play a crucial role in influencing plant diversity and plant community composition (Ehrenfeld, 2003).

Plant community composition may be more difficult to predict than the composition of plant traits within vegetation (Fukami *et al.*, 2005). In studies on plant traits most attention has been given to their relationship with ecosystem functioning for example carbon sequestration (Deyn *et al.*, 2008). However, trait groups may also be used in order to understand the response of plant communities to environmental changes (Lavorel and Garnier, 2002), but these possibilities have been less explored.

The diversity of a community can affect various ecosystem functions, including, for example, productivity (Tilman *et al.*, 1997) or resistance to invasions (Orians *et al.*, 1996). The ecosystem function is mainly a consequence of the prevailing strategies of constituent species, in interaction with the abiotic environment. Even some of the experimental effects that are ascribed to diversity are probably a consequence of the effect of abiotic conditions and species ecophysiology (Huston, 1997). However, the fact that species life histories are more important than diversity per se does not

mean that diversity has no effect on ecosystem function. Indeed, the majority of ecologists are convinced about the importance of diversity for ecosystem processes (Schlapfer *et al.*, 1999).

A growing body of evidence shows that aboveground and belowground communities and processes are intrinsically linked and that feedbacks between these subsystems have important implications for community structure and ecosystem functioning. Almost all studies on this topic have been carried out from an empirical perspective and in specific ecological settings or contexts. Due to the relatively low mobility and high survival of organisms in the soil, plants have longer lasting legacy effects belowground than aboveground (Hedlund *et al.*, 2003; Putten *et al.*, 2009).

The relationship between species diversity and ecosystem stability is controversial. Tilman *et al.* (1997) analyse biomass patterns over a decade in a grassland experiment with artificial plant communities and provide evidence for a positive relationship between the number of plant species and the temporal stability of the ecosystem. Bezemer *et al.* (2006) deduce that the temporal stability was not related to species richness, but there was a positive relationship with biomass ( $r = 0.62$ ), whereas productivity was negatively related to extinction ( $r = -0.89$ ) and colonization rates ( $r = -0.68$ ). Biomass, in turn, was strongly positively related to legume abundance ( $r = 0.82$ ), which was lowest in non-sown plots. Legume abundance therefore strongly influences relationships between diversity and functioning in plant communities, as in artificially assembled communities.

Bezemer *et al.* (2006) show that a long-term positive relationship between biodiversity and ecosystem stability also occurs in plant communities that have not been weeded after sowing. However, in the non-sown, completely self-assembled plant communities, we found that high species diversity coincided with low temporal stability and high extinction and colonization. We conclude that diversity-stability relationships are strongly context dependent.

A strong effect of species identity or functional groups was established (Huston, 1997; Symstad *et al.*, 1998; Allison, 1999) on productivity, when the models found were mainly the result of dominance of perennial sown species on the annual weeds. This find, was in agree with the hypothesis that the answer of ecosystem performance to changes of diversity was better related which species attributes than the species number per se (Chapin *et al.*, 2000; Leps *et al.*, 2001). The species richness effects may be only effective in narrow degrees of the functional composition of communities. (Tilman, 1999; Hector *et al.*, 1999), due to combination

of some factors as the species identity, effects of species attributes (Symstad *et al.*, 1998) and in the lower degree as the complementary of resource use (Hooper and Dukes, 2004).

The increase in total, aboveground and belowground biomass with grassland succession Diaz and Cabido (2001) is in agreement with earlier results for mesic environments (Gleeson and Tilman, 1990). This trend is assumed to be related to successional changes in the traits of the dominant plant species. For the three sites where biomass was sorted into grasses, legumes and non-legume forbs was observed a gradual increase in the contribution of grasses as a result of sowing and temporal development. Such a pattern is commonly found for secondary succession (Kosola and Gross, 1999). Annuals and perennials differ in characteristics related to nutrient retention and turnover, including size, relative growth rate resulting from specific leaf area and leaf nitrogen content (Garnier *et al.*, 1997), rooting depth, root to shoot ratio and foliage C/N ratio (Hooper and Vitousek, 1997). These result in a faster growth of annuals than perennials and hence greater instantaneous productivity. However, a longer growing season of perennials results in more biomass production than of annual plant species. Therefore, the relationship that we detected between biomass and relative abundance of perennials will mainly be the result of their longer growing season than of annuals.

The effects of increasing plant diversity often saturate at rather low numbers of species (in average 90% of the known cases, the productivity of the most diverse treatment is reached with mixtures of 5 species (Nijs and Roy, 2000); note that these cases may be biased). Since by definition, functional differences are larger between functional groups than between species, functional group diversity has been found to have a larger impact on ecosystem processes than species diversity (Hector *et al.*, 1999; Tilman *et al.*, 1997). In these experiments, plant functional groups have been identified on the basis of species physiology (C3 Vs. C4 species, N fixers Vs. non-N fixers, woody vs. non-woody species) or life history (early Vs. late season species, annuals Vs. perennials). However, in removal studies, plant functional traits were found to have little impact on soil communities (Wardle *et al.*, 1999).

The process responsible for the observed relationship between components of productivity and the dominance of perennials is secondary succession, where arable weeds are gradually replaced by perennial grasses and forbs (Bazzaz, 1996). These compositional changes during the early stages of succession (1 to 10-15 years) are associated with high species richness in relatively productive environments such as the ones where the sites

were located. Not surprisingly, differences in the speed of development of vegetation across sites were clearly related to site productivity, resulting from abiotic conditions and agricultural practices prior to abandonment (Huston, 1994).

Processes within ecosystems can depend on the diversity of the organisms which constitute them. Recent experiments have disclosed which processes tend to rely on species richness and what the shape of these relationships is (Symstad *et al.*, 1998). In addition, first assessments have been made of the significance of functional groups to ecosystem processes and of the relative importance of species composition vs species number (Hooper and Vitousek, 1998; Nijs and Roy, 2000).

As empirical evidence accumulates, the paucity of mechanisms to explain the influence of species diversity on ecosystem function becomes apparent. Hypotheses have been proposed essentially for productivity, for example having more species could give access to more resources provided that species are complementary in resource use in time or space (niche differentiation). An alternative explanation is that having more species increases the probability of including a single productive species (the sampling effect: Huston, 1997; Aarsen, 1997).

The experimental manipulation of (Diaz and Cabido, 2001) aiming at accelerating succession succeeded in terms of achieving the desired species composition (Putten *et al.*, 2000), as well as in terms of enhancing the development of ecosystem processes, such as biomass production, Light Interception (LAI) and photosynthetic activity. In their data, the effects of secondary succession were evidenced in two ways. First across treatments that in fact represented early and mid-successional stages of vegetation development. Second through the three-year course of the experiment, where temporal increases in the dominance of sown perennials resulted in further increases in biomass accumulation.

### 1.8. Biotic Factors

While the diversity-productivity debate has been focused on plants mainly, little attention has been given to possible consequences of plant species diversity for soil communities under field conditions (Wardle, 2002; Hedlund *et al.*, 2003). While the effects of plant diversity on conversion and retention of energy and nutrients in soil is due to soil organisms mainly (Wardle *et al.*, 1997; Hooper *et al.*, 2005), the response of the different trophic levels in the soil community to plant diversity and productivity is rather inconclusive. The microbial community shows either a positive relation

(Wardle and Nicholson, 1996; Wardle and Lavelle, 1997; Bardgett *et al.*, 1999; Wardle *et al.*, 1999; Broughton and Gross, 2000; Donnison *et al.*, 2000) or no response (Wardle *et al.*, 1997; 1999) to diversity and productivity of the plant community.

It is an even more complex task to predict the effects of the plant community on higher trophic levels of a soil community, as interactions between trophic levels can be controlled not only by bottom-up but also by top-down interactions (Schaefer, 1995; Rüter *et al.*, 1995; Mikola and Setälä, 1998). Most studies on the relationship between plant diversity and soil animal abundances seem rather inconclusive or with no direct correlations (Wardle *et al.*, 1999). Although, it has sometimes been suggested that higher trophic levels are more strongly affected by plant diversity changes than lower trophic levels such as microorganisms (Spehn *et al.*, 2000; Mikola *et al.*, 2001).

### 1.9. Implications for the Restoration of Species Rich Grasslands on Ex-Arable Land

The results of (Diaz and Cabido, 2001) show that sowing mixtures of later successional plant species may enhance the initial functional diversity of plant species by stimulating the establishment of mid-successional perennials. This may have undesirable side effects through the introduction of alien genotypes, but it enhances the exclusion of arable weeds (Putten *et al.*, 2000) and high diversity mixtures enhance the reliability of ecosystem functions (Leps *et al.*, 2001). Introduction of mid-successional plant species stimulates the restoring of ecosystem processes, such as efficient light capture (LAI) and light utilisation (photosynthesis) and it affects aboveground insect assemblages. However, the short-term effects of the experimental treatments on different trophic groups of nematodes (Korthals *et al.*, 2001) and on microbial activity (Maly *et al.*, 2000) are limited. In fact, in the first two years, the effect of ending agricultural practices alone had much larger effects on the soil community than any of the experimental manipulations of the plant assemblages (Maly *et al.*, 2000; Korthals *et al.*, 2001). Effects of plant species diversity on soil processes (e.g., decomposition) in Swiss biodiversity fields (Spehn *et al.*, 2000) seem to be due to more extreme plant diversity treatments and to the influence of nitrogen fixing plant species on soil properties.

Successful establishment of a perennial-dominated, productive cover may be more adequate for the extraction of excess nutrients from agricultural soils, however, this did not appear in short-term nitrification measurements (Maly *et al.*, 2000). Mowing may be

required in order to remove the nutrients conserved in labile organic matter, but it will be less supportive to the restoration of soil carbon levels. It is open to question whether manipulations such as the ones applied in our experiment, may drive old-field ecosystems faster towards higher sequestration states, before being able to assess the benefits for the mitigation of global environmental change (esp. CO<sub>2</sub> and nitrogen deposition) (Fan *et al.*, 1998).

In some parts of the world, such as in North America and Europe (Turner *et al.*, 1990), there is an opposing trend, towards set-aside policies and the abandonment of agricultural land. Land abandonment provides opportunities to restore ecosystem properties such as biodiversity and biogeochemical cycles. However, recovery of pre-agricultural soil conditions can be very slow (e.g., about 200 years for soil carbon and nitrogen, (Knops and Tilman, 2000)). The restoration of former species diversity is often constrained by abiotic and biotic conditions, such as eutrophication or seed bank depletion (Bakker and Berendse, 1999). In the mean time and especially in the years just after abandonment, unmanaged land may favour nutrient leaching, constitute reservoirs of aggressive weeds damageable to adjacent fields and alter the aesthetics of the landscape.

## 2. CONCLUSION

Succession at abandoned arable land may be enhanced by the introduction of later successional plant species. Moreover, some stage of succession the plant species diversity present may determine how succession proceeds. Local conditions and species identities affect the suppressive capacity of plant communities.

Many functional characteristics of ecosystems are in some way connected to productivity and, because of the strong effect of productivity on diversity, it is extremely difficult to interpret correlations between diversity and the functioning of ecosystems. Early- and late-successional communities differ not only in their stability characteristics and also in their species richness.

The development of the community is often affected by the presence of strong dominants. This part of the course of the community development is highly idiosyncratic, as it depends on the local conditions and on the presence of a species able under given condition attain high dominance.

There is very little evidence of effects of plants species diversity treatments on soil communities from biodiversity experiments in the field. The field sites

should be subjected to soil sterilization or to top soil removal in order to reduce the work load of weeding. Management by mowing of plots will probably delay the effects of the plant communities on the soil community development.

Sowing mixtures of later successional plant species may enhance the initial functional diversity of plant species by stimulating the establishment of mid-successional perennials, this may enhance the exclusion of arable weeds. Introduction of mid-successional plant species stimulates the restoring of ecosystem processes, such as efficient light capture (LAI) and light utilisation (photosynthesis) and it affects aboveground insect assemblages.

Successful establishment of a perennial-dominated, productive cover may be more adequate for the extraction of excess nutrients from agricultural soils. Mowing may be required in order to remove the nutrients conserved in labile organic matter, but it will be less supportive to the restoration of soil carbon levels.

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