Chapter 7

Functional Diversity – at the Crossroads between Ecosystem Functioning and Environmental Filters

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7.1 Introduction

Functional diversity, i.e., the *kind*, *range*, and *relative abundance* of functional traits present in a given community, is one of the major factors influencing ecosystem functioning (Chapin et al. 2000b; Díaz and Cabido 2001; Loreau et al. 2001; Hooper et al. 2005). Through its effects on ecosystem functioning, plant functional diversity (hereafter FD) is both affected by and affects all the major global change drivers identified by the international scientific community (Fig. 7.1, path 1). Changes in climate, atmospheric composition, land-use and distur-

bance regime, and biotic exchanges (deliberate or accidental introduction of organisms to an ecosystem) all have non-random effects on FD, i.e., they select for or against species bearing certain traits. For example, the more drought- and/or frost-sensitive species are eliminated first under an increased frequency of climatic extreme events (Díaz et al. 1999). Slow-growing species are eliminated when ecosystems experience nitrogen loading (Thompson 1994). Non-resprouting species are strongly reduced by increased fire return intervals (Russell-Smith et al. 2002; Johnson and Cochrane 2003). At the same time, through its effect on ecosystem processes, FD influences climate, carbon exchange with the atmosphere,

Fig. 7.1.
Functional diversity is both a response variable modified by, and a factor modifying global change drivers. *Solid arrows* indicate relationships addressed in this chapter. See text for description of numbered links
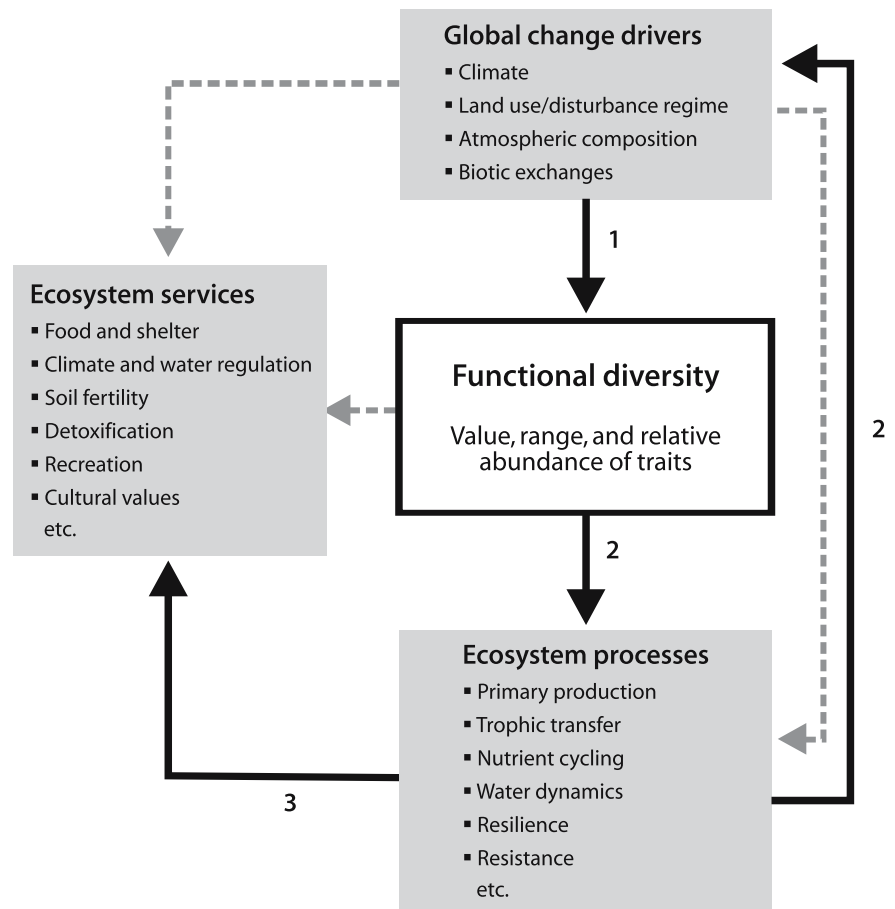
disturbance regime, and the susceptibility to, and consequences of biotic exchanges (Fig. 7.1, path 2). In this chapter we focus on the processes of mutual influence and feedbacks between global change drivers and FD, and discuss the empirical evidence supporting the effect of different components of FD.

7.2   Environmental Filters Affect FD

FD at any site is the result of the action of environmental filters on the regional species pool. Environmental filters are non-random factors that narrow the range of functional traits in a local community. Filtering operates primarily at the level of ecological sorting (i.e., changing the proportions of different genotypes represented in the established community, but not altering the genotypes themselves), but can lead to stabilizing or directional natural selection over evolutionary time. Climate, disturbance regime, some aspects of atmospheric composition, and biotic interactions are major environmental filters (Keddy 1992; Woodward and Diament 1991; Díaz et al. 1998, 1999), and strongly determine which traits and functions can survive at any particular site. It has been suggested that, at a given site, species richness is limited by the regional species pool, whereas functional diversity is limited by local conditions that determine the availability of niches (Schmid et al. 2002).

The four major global change drivers can be interpreted as environmental filters: they filter out organisms bearing certain sets of traits and allow the establishment, persistence and spread of others (see Lavorel et al. 2007, Chap. 13 of this volume, for more examples of environmental filtering of plant functional traits). Therefore, the dramatic biodiversity loss now experienced at the global scale has two aspects: random extinction as a result of the reduction of inhabitable area (i.e., as expected on the basis of island biogeography theory; MacArthur and Wilson 1967), and non-random global or local extinction as a result of the filtering effect of global change drivers. The latter leads to a biota that not only is taxonomically poorer, but also represents a *biased* subset of the range of traits initially available. Recent assessments have shown strong asymmetries in the extinction risk of species with certain traits (McKinney and Lockwood 1999), or belonging to different habitats (Brook et al. 2003) or biomes (Thomas et al. 2004). Fragmentation because of land use, as well as increasing the random probability of extinction, differentially increases the local extinction risk of certain species, by altering water, wind, nutrient dynamics and flammability (Cochrane et al. 1999). Biotic homogenization, i.e., the replacement of local biotas with widespread non-indigenous species due to habitat modification and transportation of exotic species, is also a process where 'winners' and 'losers' bear different traits (McKinney and Lockwood 1999; see also Vilà et al. 2007, Chap. 8 of this

volume). Non-random extinctions and functional shifts in vegetation cover as a consequence of the filtering effects of global change drivers are at least as alarming as global extinctions due to reduction in habitat area. This is because their potential effects on ecosystem processes and services (Fig. 7.1, paths 1, 3), and feedbacks to global environmental drivers (Fig. 7.1, path 2) can be dramatic well before species disappear from the face of the Earth.

7.3   FD effects on Global Change Drivers

Although the evidence of effects of FD on global change drivers and ecosystem services mediated by altered ecosystem functioning is accumulating fast, it is not equally strong for the different components of FD. Theory suggests that the kind, relative abundance, and range of traits present in a community should affect ecosystem processes and thus ecosystem services and global change drivers. However, at present there is much more empirical support for the role of the traits of the dominants (*kind* and *abundance* of traits) than for that of the *range* of traits present. On the other hand, although many (and sometimes dramatic) examples suggest that indirect interactions are crucially important in triggering some ecosystem-level feedbacks, there is still no integrated theoretical framework explicitly linking FD with these feedbacks, or predicting the consequences of indirect interactions in systems with different degrees of FD. In this section, we summarize some basic theoretical issues and the empirical evidence related to each of these components.

7.3.1   The Traits of the Dominants

Despite some remaining controversy on precisely which mechanisms explain diversity effects on ecosystem functioning (see Hooper et al. 2005 for an updated review), most researchers now recognize that FD is more relevant to local-scale ecosystem functioning than taxonomic diversity (Grime 1998, 2002; Chapin et al. 2000b; Díaz and Cabido 2001; Loreau et al. 2001; Tilman 2001; Naeem and Wright 2003; Petchey 2004; Petchey et al. 2004; Hooper et al. 2005). The fact that species show different attributes, and thus their contributions to ecosystem processes are not equal or interchangeable, is at the heart of the mechanisms proposed to explain how biodiversity should affect ecosystem processes. However, most studies of the effects of diversity on local-scale ecosystem functioning have considered only species richness, or have taken a very coarse approach to FD. For example, they consider a small number of life forms or taxonomic groups (e.g., grasses, legumes, composites), all of them with similar abundances (see Box 7.1 for a discussion of links between species richness and FD, and issues involved in FD measurement).

Box 7.1. Measuring FD

Despite the widely recognized importance of FD in determining ecosystem processes, species richness (number of species present in a given community) continues to be the most used and manipulated measurement of diversity (Díaz and Cabido 2001; Petchey 2004). This is partly because of practical reasons. First, it is much easier to count species than to weigh them by their abundance. However, this means in practice ignoring the fact that the effect of a species in an ecosystem is largely a function of its biomass (see Sect. 7.3.1). Giving the same 'weight' to extremely abundant and extremely rare species, as happens in species richness, can substantially obscure links between diversity and ecosystem processes. Second, the objective quantification of FD is far from straightforward. The most common measurement of FD is functional type richness, but the results strongly depend of the grouping into functional types (Díaz and Cabido 2001; Petchey 2004), which may or may not reflect true functional differences among species and in any case makes comparisons among different studies extremely difficult. The most promising methods of quantifying FD thus appear to be those based trait distances between species (Díaz and Cabido 2001; Naeem and Wright 2003; Petchey 2004). These require the measurement (or literature compilation) of the attributes of many species, which is time- and resource-consuming. Also, there is so far no ideal FD index, since none of the available metrics can simultaneously account for functional distances between species independently from species richness and at the same time deal with multidimensional- attribute spaces (see Mason et al. 2005, Petchey et al. 2004 and Moulliot et al. 2005 for thorough comparison of indices). Moreover, even an index with all the desirable properties (e.g., those enumerated by Mason et al. 2005) would be of little use if it is not based on functionally important traits (see Table 7.1 and Lavorel et al. 2007, Chap. 13 of this volume, for examples of 'relevant' traits for different ecosystem processes).

Beyond practical considerations, the use of species richness as a surrogate for FD is based on assumptions, which are unrealistic for most natural ecosystems (Díaz and Cabido 2001; Naeem and Wright 2003). FD is often assumed to vary in direct proportion to species diversity (Lawton et al. 1998; Tilman 1999; Naeem 2002). Species richness should be an adequate surrogate for func-

tional richness only if there is a linear increase in niche space occupation as species richness increases. Theoretically, this can happen only when there is random (Fig. 7.2a) or uniform (Fig. 7.2b) occupation of niche space (Díaz and Cabido 2001), and when all species are equally different (addition of any species to a community and the contribution of each species to functional diversity is independent of species richness (Naeem and Wright 2003). However, these cases are uncommon in nature, as compared to aggregate occupation of niche space (Holling et al. 1996). This is because in nature random assemblage and extinction are much less common than non-random ones (Zobel 1997; Díaz and Cabido 2001; see also Sect. 7.2). When aggregate occupation of niche space is related to strong convergence of different species into contrasting functional types [e.g., annual graminoids, succulents and dwarf shrubs in deserts, Fig. 7.2c], species richness overestimates functional richness. When aggregate occupation of niche space is due to strong differentiation in niche space among different genotypes or phenotypes within a single species (e.g., herbivore-tolerant and herbivore-intolerant grass genotypes in prairie-dog dominated landscapes, Jaramillo and Detling 1988; intraspecific differentiation of the tree *Metrosideros polymorpha* in the Hawaiian islands, Cordell et al. 1998), species richness underestimates functional richness. These mismatches between taxonomic and functional richness can have important practical consequences. Only in cases in which extinction is happening at random (and presumably in associated ecosystem functioning) with species richness loss. In other cases, the consequences of extinctions will likely be non-linear. For example, in the case illustrated in Fig. 7.2d, an assessment of species number loss could grossly underestimate functional richness loss. Biodiversity assessments based only on species richness and checklists will tend to overlook processes of functional extinction, that is, the extinction of local genotypes or phenotypes without immediate risk of global (Estes et al. 1989; Luck et al. 2003), Functional extinction often leads to ecosystems that retain the same richness and taxonomic composition of species, but cannot sustain necessary functions for their long-term persistence (e.g., the 'half-empty forest' of Redford and Feinsinger 2001).

Fig. 7.2.
Extreme cases of links between plant species richness and functional richness. *Axes 1* and *2* in the *shaded rectangles* represent different resource or disturbance axes. *Solid-line circles* represent the fundamental niches of different species; *dashed-line circles* represent the niche of different genotypes, phenotypes or ontogenetic stages within a single species (reprinted from Díaz and Cabido 2001, with permission from Elsevier)
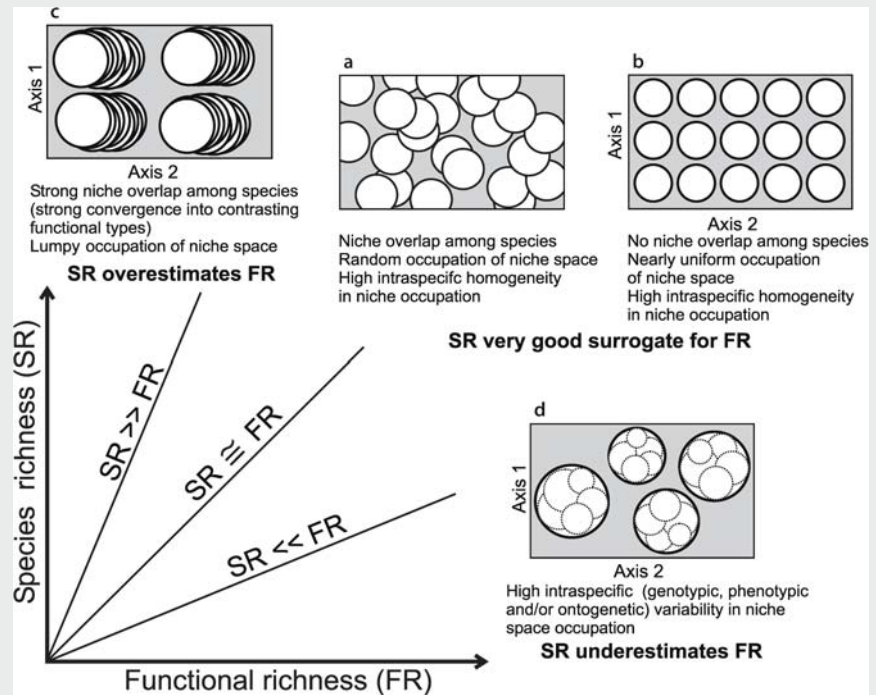
In an analysis of synthetic-community and field experiments involving plants, Díaz and Cabido (2001) found that rates and magnitudes of ecosystem processes, such as plant and soil biomass production, decomposition, mineralization or various aspects of stability, were more consistently associated with functional composition (presence of certain *kinds* of plant functional traits; e.g., species with nitrogen-fixing symbionts, or with particularly fast growth rate, or evergreen leaves) and functional richness (number of different plant functional types) than with species richness. Functional composition was associated with ecosystem processes more often than was functional richness, even though most of these experiments kept the relative abundance among species unnaturally even (but see Petchey's 2004 considerations on the assignment of species to functional groups). This can hardly come as a surprise. The fact that the morpho-functional traits of the dominant plant species strongly determine ecosystem properties has been recognized since the earliest days of ecology, and has often been referred to as the 'mass-ratio' hypothesis (Grime 1998). Locally abundant plant traits determine the rate and magnitude (Grime 1977; Hobbie 1992; Chapin et al. 1993; Aerts 1995; Aerts and Chapin 2000; Herbert et al. 1999; Lavorel and Garnier 2002; Díaz et al. 2004; Garnier et al. 2004), and stability (Lepš et al. 1982; McGillivray et al. 1995; Grime et al. 2000) of major ecosystem processes. The existence of recurrent suites of plant traits (e.g., 'acquisitive' vs. 'conservative' syndromes) with predictable controlling effects on ecosystem processes such as primary production, trophic transfer, carbon storage, or nutrient cycling has been proposed (Grime 1977; Chapin 1980; Chapin et al. 1993), and empirically supported at the local (e.g., Chapin et al. 1996; Grime et al. 1997; Garnier et al. 2004) and trans-regional levels (e.g., Díaz et al. 2004).

By affecting ecosystem processes, the traits of the dominant plant species (i.e., *kind* and *relative abundance* of traits) have considerable impact on ecosystem services and therefore human well-being (Fig. 7.1, path 3; Table 7.1). On the other hand, global change drivers affect, and to a certain degree are affected by, locally dominant plant traits (Fig. 7.1, paths 1 and 2). The FD approach thus offers the interesting perspective of tracing some causal relationships and mutual feedbacks between global change drivers, locally dominant plant traits, ecosystem properties, and ecosystem services.

Table 7.1. Causal connections between some individual plant traits, ecosystem processes, and ecosystem services. *ES* = ecosystem service. ES classification follows MEA (2003)

Individual traits	Ecosystem processes	Ecosystem services
Leaf nutrient concentration Leaf toughness Specific leaf area Leaf turnover rate	Net primary productivity Relative productivity rate Consumption by herbivores ungulates (trophic transfer) Decomposition and net mineralization	Soil formation and fertility Food and fiber production Carbon sequestration Resistance of production of goods and services over time Cultural and aesthetic ES (e.g. autumn colours, traditional ungulate-dependent landscapes)
Canopy size Leaf phenology Leaf distribution over stems Growth form Canopy architecture	Evapotranspiration, heat exchange Albedo, roughness	Climate regulation
Shoot height Wood density Lifespan Leaf nutrient concentration	Accumulation of standing biomass	Carbon sequestration Climate regulation (indirectly by carbon sequestration)
Tissue water content Canopy architecture Leaf nutrient and resine content Texture and architecture of litter	Vegetation flammability Fuel load (undecomposed litter) Soil insulation from air temperature and moisture	Nutrient cycling Soil formation, fertility and stability Climate regulation Carbon sequestration Resilience of ES over time
Seed shape and mass	Persistence in the soil seed bank Seed transport by animals	Resilience of production of goods and services over time Maintenance of food-provisioning and cultural ES mediated by animals
Root depth Root architecture	Evapotranspiration Soil exploration by root systems	Climate regulation Water runoff Soil stability

7.3.1.1 *FD and Climate*

FD both responds to and affects the climate system. Local FD is strongly determined by the climatic filter (Fig. 7.1, path 1; Lavorel et al. 2007, Chap. 13 of this volume). In addition, FD affects climate regulation, which is one of the most essential services that natural ecosystems provide to humans (MAE 2003; Fig. 7.1, path 3). FD affects climate indirectly, through changes in the carbon sequestration capacity of the biota (i.e., the more carbon biological systems can sequester, the less will be contributed to the greenhouse effect in the atmosphere), and also directly, through changes in the biophysical properties of the land surface. Not surprisingly, these effects are most pronounced where the ecological changes occur over large areas. For example, in northeast Siberia, widespread fires and other disturbances lead to a replacement of mosses and evergreens, which have a long season (but low rates) of photosynthetic activity, with deciduous plants that have a shorter season (and higher rates) of photosynthesis. Mosses also insulate the soil, so the depth of soil thaw is shallower and soil respiration is less, particularly in late summer and early winter. The net effect of disturbance-induced changes in FD is therefore to increase the magnitude of both summer carbon gain and winter carbon loss. In this way recent increases in disturbance contribute to the increased seasonal amplitude of atmospheric carbon dioxide concentration at high latitudes (Zimov et al. 1999). The feedback from increased carbon dioxide to climate occurs at the global scale because of the rapid mixing of the atmosphere.

FD also interacts with the climate system through changes in water and energy exchange (Foley et al. 2003). Complex canopies often absorb more energy (have a lower albedo) because canopy complexity increases the probability that other surfaces will absorb reflected radiation before it is lost to space. For this reason there is a decrease in albedo from conifer forests to deciduous forests to grasslands. Particularly in open-canopied ecosystems, which account for 70% of the ice-free terrestrial surface (Graetz 1991), species in the ecosystem will likely influence stand-level albedo, with their importance depending on abundance, height, and structural properties. In addition, diversity often contributes to the structural complexity of leaf arrangement in canopies and therefore the efficiency with which incoming radiation is trapped. For example, the increase in shrub density in arctic tundra in response to regional warming (Sturm et al. 2001) has reduced regional albedo and increased regional heating (Chapin et al. 2000a). Structural diversity of the canopy also increases the efficiency with which heat and moisture are transferred to the atmosphere. Even a low density of trees (e.g., <100 ha^{-1}) in a savanna or woodland substantially increases turbulent exchange with the atmosphere (Thompson et al. 2004).
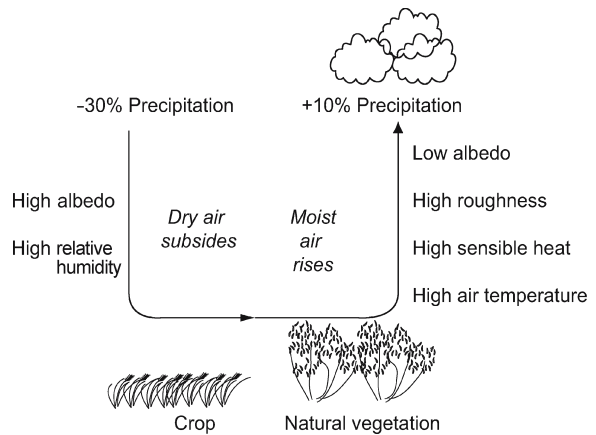

Fig. 7.3. Effects on regional climate of conversion of heathland to croplands in southwestern Australia (Chambers 1998) (reproduced from Chapin et al. 2002, with permission from Springer-Verlag)

The diversity of patches on a landscape exerts an additional impact on biophysical coupling between land and atmosphere. Patches that are larger in size than the depth of the planetary boundary layer (i.e., their smallest dimension is at least 10 km) and which differ in albedo or surface temperature from neighboring patches create convection cells, in which air rises above the warm patch; this air is replaced by cooler moister air that flows laterally from adjacent patches (Pielke 2001). In Australia, for example, the replacement of native heath vegetation by croplands increased regional albedo. As a result, air tended to rise over the dark heathland, drawing moist air from the croplands to the heathlands. The net effect was a 10% increase in precipitation over heathlands and a 30% decrease in precipitation over croplands (Fig. 7.3) (Chambers 1998).

7.3.1.2 *Fd and Land-Use/Disturbance Regime*

Changes in FD brought about by shifting climatic or land-use conditions can in turn produce changes in an ecosystem's disturbance regime and/or resource basis, and thus its ecosystem-service value and suitability for certain land uses. These include, for example, changes in carrying capacity for livestock, capacity for water retention and flood regulation, control of human and domestic animal disease, or amenity values. These processes sometimes start with sharp increases in abundance of native species that were previously non-dominant (e.g., woody encroachment; Scholes and Archer 1997) or the spread over the landscape of exotic species. The latter is the result of the explosive increase in biotic exchanges during the 19th and 20th centuries, often in combination with changes in climate and land use (Fig. 7.1, path 1; see Vilà et al. 2007, Chap. 8 of this volume). Once established, some exotics become invasive and alter ecosystem productivity, resource dynamics, stability, and disturbance

regime, often irreversibly (Fig. 7.1, paths 2 and 3). A review of over 150 studies to evaluate the mechanisms underlying the impacts of exotic plant invasions on plant and animal community structure, nutrient cycling, hydrology, and fire regimes revealed that studies examining effects of invaders on ecosystem processes often tend to attribute impacts to differences in important functional traits of the invader as compared to the resident species (Levine et al. 2003). The majority of examples where significant effects on ecosystem processes were reported concerned invasions by a life form previously absent from a native ecosystem (e.g., grasses) and species with traits allowing them to tap into unexploited resources (e.g., nitrogen-fixing, deep rooting). However, life forms readily present in an ecosystem could also have impacts, e.g., on the nitrogen cycle or fuel accumulation for fire, when invaders had attributes conferring them greater efficiency in resource use than the natives.

A recent study illustrates how climate and land-use change and biotic exchanges can alter, and be altered by FD, in a feed-forward, highly irreversible process. The northern Mediterranean basin agricultural land abandonment over the last century (Moreno et al. 1998) and ongoing climate change (Pausas 2004) have resulted in increasing frequencies of very large, intense fires. In Catalonia (NE Spain), higher fire frequency seems to promote the expansion of the large, evergreen, resprouting tussock grass *Ampelodesmos mauritanica* (Vilà et al.

2001). Near-monocultures of *A. mauritanica* now occupy original shrubland sites. Grigulis et al. (2005) tested the hypothesis of a positive feedback between *A. mauritanica* abundance and changing fire regimes by combining measurements across a natural gradient of density of *A. mauritanica* near Barcelona, Spain with model simulations of fire and vegetation dynamics using the landscape modeling platform LAMOS (Lavorel et al. 2000; Cousins et al. 2003). The invasion of shrublands by *A. mauritanica* produced a series of spectacular modifications in community structure and ecosystem properties, which translated to changes in vegetation and fire regimes at the landscape-scale (Fig. 7.4):

1. Aboveground biomass nearly doubled in plots with high vs. low density of *A. mauritanica* (Fig. 7.4a). This occurred because *A. mauritanica* replaced native shrubs, but also some grasses and herbs, and also because the standing biomass of *A. mauritanica* increased significantly. Therefore the morphological/functional composition of the community was considerably modified by the invasion. The quantity of litter also increased significantly, leading to much higher total fuel loads in high invasion plots. The specific aboveground net primary productivity (Garnier et al. 2004) of all components of the community decreased significantly with increasing density of *A. mauritanica*.
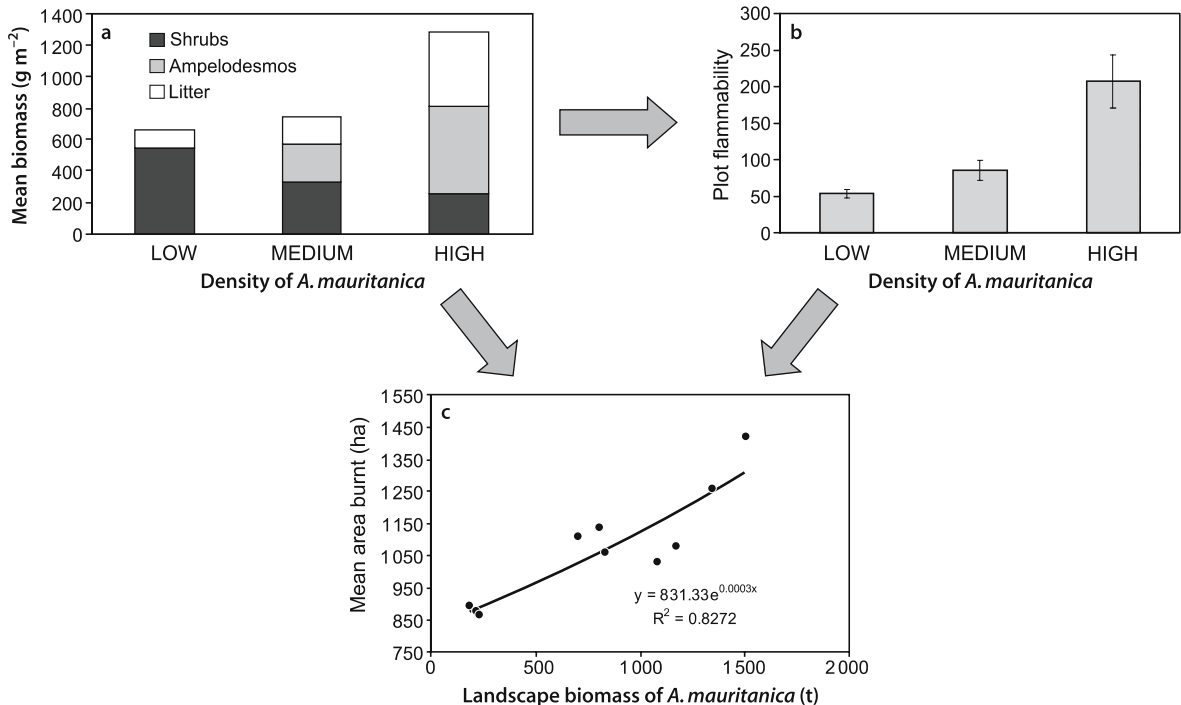

Fig. 7.4. Positive feedback between fire regimes and invasion by *Ampelodesmos mauritanica* in Catalonia. **a** Functional composition of communities with increasing density of *A. mauritanica*. **b** Plot-level flammability calculated from individual flammabilities weighed by the relative biomass contributions of species. **c** Effect of total biomass of *A. mauritanica* on mean area burnt during fire years (reprinted from Grigulis et al. 2005, with permission from Blackwell)

2. The considerable litter accumulation observed with increasing density of *A. mauritanica* was explained not only by the greater production of litter, but also by the fact that its litter decomposed at a 30% slower rate than that of the resident shrubs.

3. Under standardised conditions, *A. mauritanica* ignited much more rapidly than any of the shrub species, especially its dry litter, and once burning produced a more intense flame, again especially as litter. Calculated plot flammability taking into account changes in functional composition and specific flammabilities showed a >40-fold increase from low- to high-density plots (Fig. 7.4b).

4. Simulations of coupled vegetation- fire dynamics parameterised from these measurements of ecosystem properties and life history characteristics of *A. mauritanica* showed that invasion success and contribution to community biomass of *A. mauritanica* increased abruptly with decreasing fire return intervals. Total area burned in the landscape during each fire year was positively and exponentially related to the total biomass of *A. mauritanica* present in the landscape (Fig. 7.4c). Landscapes can hence switch from regimes of small localized to extensive fires as a result of the spread of *A. mauritanica* under decreasing fire return intervals. These patterns were explained by the increasing connectivity of highly flammable vegetation as *A. mauritanica* becomes more frequent in the landscape, coupled with the direct positive effects of fire on the demography of this grass.

5. Hence invasion of Catalan shrublands by *A. mauritanica* threatens a range of services that these natural ecosystems provide to rural and urban populations. Greatest of these is exposure to wildfire, especially in suburban areas that surround the city of Barcelona. Effects on native biodiversity were not yet detectable for plants, but may occur at later stages of invasion, in particular via the notable changes in fire regimes. Finally, invasion by *A. mauritanica* is perceived by the local population and managers as a threat to landscape amenity value.

7.3.2   The Role of Interactions

We have shown above that three components of FD – the *kind*, *relative abundance* and *range* of traits – are important in explaining biodiversity effects on ecosystem processes. In Sect. 7.3.1 we presented strong evidence of the role of the first two components: at any particular location, and within the envelope defined by climatic and disturbance conditions, ecosystem functioning is largely driven by the attributes of the dominant species, which are in turn strongly determined by the action of environmental filters. We know much less, however, about the functional role of the *range* of traits present in any

given ecosystem, i.e., does it matter whether the organisms present are very similar or very different in terms of functional traits? The overwhelming evidence in favor of the mass-ratio hypothesis, which states that instantaneous functioning of ecosystems is determined to a large extent by the trait values of the dominant contributors to plant biomass; Grime (1998), might lead to the conclusion that the ecosystem role of subordinate species can be safely considered negligible. However, both theoretical knowledge of interactions and empirical examples tell us otherwise. Subordinate species are known – or expected – to play a significant role in long-term ecosystem stability (see e.g., Grime 1998; Dukes 2001; Lyons and Schwartz 2001; Lyons et al. 2005). Interactions between dominant and subordinate species within a given trophic level, and across trophic levels, are at the core of some of the mechanisms by which biodiversity affects ecosystem functioning (Chapin et al. 2000b). Two mechanisms involving species coexistence within the trophic level of primary producers are based on trait differences (*range* of traits) among species. These are resource use complementarity and facilitation.

Resource use complementarity is based on temporal and spatial niche partitioning (e.g., different rooting depths, phenologies, establishment mechanisms in regeneration gaps, forms of nitrogen that can be taken up from the soil), which reduces interspecific competition (MacArthur and Levins 1967). As a mechanism by which biodiversity influences local-scale ecosystem functioning, resource use complementarity assumes that the larger the functional trait distance between plants, the stronger the complementarity effect, and the more complete the total resource use by the community is expected to be (Trenbath 1974; Ewel 1986; Vandermeer 1989; see Hooper et al. 2005 for a detailed review). Complementarity in resource use is indeed a common coexistence mechanism in plant communities (e.g., Silvertown et al. 1999; McKane et al. 2002; Hooper and Dukes 2004). However, it is still uncertain whether this higher FD consistently leads to higher ecosystem 'performance' (e.g., higher productivity, nutrient retention, stability) beyond combinations of a very small number of species, such as those found in agriculture and forestry. Many cases in which species differences lead to higher biomass production involve nitrogen-fixing legumes, and thus can be interpreted as facilitation (Fridley 2001, see below).

Complementarity in resource use leading to higher ecosystem 'performance' in the absence of nitrogen-fixing legumes has been empirically demonstrated in some cases (e.g., van Ruijven and Berendse 2003), but seems far from universal, and its importance likely depends on the environmental context (Fridley 2003; Dimitrakopoulos and Schmid 2004; Hooper and Dukes 2004; Petchey 2004; Hooper et al. 2005). Grime (2002) has argued that, while resource use complementarity is definitely important as a coexistence mechanism, there is no reason based on

natural selection why it should lead to 'enhanced' ecosystem functioning. The admission and persistence of organisms in plant communities and ecosystems depend upon their individual fitness rather than their contribution to community- or ecosystem-level properties, and coexistence and contribution to ecosystem processes often depend on different plant traits. Whereas complementarity facilitates the entry and persistence of species in the community it cannot be assumed that this will necessarily lead to complementary roles in sustaining the ecosystem. For example, Hooper and Dukes (2004), using synthetic serpentine-grassland communities, found that functional trait differences among species lead to strong complementarity in resource use among plants, but these were not sufficient to cause consistent increases in community productivity with increasing number of species. Dimitrakopoulos and Schmid (2004) measured biodiversity effects on plant biomass in synthetic calcareous-grassland communities planted on soil of different depths, and found that the importance of resource use complementarity increased as soil depth increased, suggesting that the biodiversity effect on biomass production may be strongly constrained in shallow soils.

The second interaction-based mechanism by which trait differences between species within the same trophic level can influence local-scale ecosystem functioning is facilitation. Probably the best example of this is the frequent stimulation of total production of species mixtures in the presence of nitrogen-fixing species. This is well known from the agricultural and forestry literature (Trenbath 1974; Vandermeer 1989; Cannell et al. 1992) and has been one of the most consistent effects of FD in synthetic-community experiments on the role of diversity in local-scale ecosystem functioning. Other plant-plant facilitation examples are the nurse effect by which larger plants ameliorate harsh climatic conditions or herbivore pressure for seedlings of other species (see Callaway 1992 and Bruno et al. 2003 for examples and detailed review of other facilitation mechanisms). Despite the increased interest in facilitative interactions in the past few years, there are not many documented examples of effects at the level of ecosystem functioning beyond biomass production (often positive effects, see above) and invasion resistance (both positive and negative effects; see Marler et al. 1999; Stampe and Daehler 2003). The literature on the effects of facilitation or resource use complementarity on ecosystem ser-

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Box 7.2. Indirect interactions challenge the FD approach

Indirect interactions are those in which a species, through direct interaction with another species or modification of resources, alters the abundance of a third species with which it is not directly interacting. Such interactions challenge the FD approach, since there is no way to predict the ecosystem-level consequences of species additions or loss on the basis of the kind, range or relative abundance of traits.

Example 1
Facilitation among Woody Invaders in Temperate and Subtropical South America

The glossy privet (*Ligustrum lucidum*) is an evergreen, bird-dispersed and shade-tolerant Asiatic tree that invades seminatural woodlands and grasslands in southern South America. Originally introduced as an ornamental plant, this species apparently does not grow faster than native species, nor can it use soil resources not taken up by the resident communities (Gurvich et al. 2005). Its seedlings are susceptible to grazing by livestock and its recruitment has been reported to be strongly limited by the availability of recruitment micro-sites and by the interference from herbaceous vegetation (Mazia et al. 2001). On these bases, one would hardly predict its aggressive expansion over the landscape in the last decades. In central Argentina open woodlands its success is the result of indirect interactions with the native fauna and flora, mediated by the presence of another woody invader, the fire hawthorn (*Pyracantha angustifolia*). Unlike native species, both exotic shrubs produce fleshy fruits in autumn and winter, thus offering an extra food source to native frugivorous birds during a period of scarcity (Tecco et al. 2006). The branching architecture of *P. angustifolia* is attractive to perching birds, thus facilitating the dispersal of *L. lucidum* seeds under its canopy. Once germinated, *L. lucidum* seedlings grow slowly under *P. angusti-folia*, but as a shade tolerant, survives much better than the herbaceous dicots and grasses which outcompete it in the open (Tecco et al. in press). Also, the thorny, dense, umbrella-like canopy of *P. angustifolia* protects the seedlings from browsing and trampling by livestock. Once established, *L. lucidum* forms dense, shady, almost impenetrable

thickets with an extremely poor understorey, both in terms of biomass and species richness (Lichstein et al. 2004). This, in turn, is expected to have important effects on ecosystem processes, services, and the land-use value of the land. For example, the total standing biomass and water uptake of *L. lucidum* near-monocultures are likely to be higher than those of stands dominated by semideciduous native vegetation. Carbon and nutrient cycling may also change by alteration of decomposition processes through altered litter quality and quantity and by a cooler, moister microhabitat. The effect of the winter extra supply of food for frugivorous birds by these two invasive species can have ripple effects on bird communities and the fleshy-fruited species dispersed by them.

Example 2
Gophers and Goatgrass in Californian Grasslands

The expansion of the exotic barbed goatgrass (*Aegilops triuncialis*) over the Californian landscape is also the consequence of several indirect interactions between three trophic levels that can hardly be predicted on the basis of the traits of the dominant species or the range of traits present in the community. According to Eviner and Chapin (2003), gophers are both attracted to patches dominated by goatgrass and negatively affect the latter. Apparently, the root architecture of goatgrass stabilizes the soil and makes it more efficient for gophers to burrow in patches dominated by this species. The negative effects of gophers on goatgrass stem from two processes. First, their burrowing activity buries goatgrass plants and thus slows down its expansion over the landscape. Second, they reduce the infection of goatgrass seedheads by the fungus *Ulocladium*, thus retarding germination and putting this species in a disadvantaged position with respect to native grasses. On the other hand, the presence of gophers decreases with heavy grazing. The expansion of goatgrass in heavily grazed paddocks decreases both the pastoral quality (seedheads can cause injury to livestock and its leaves are very poor nutritionally) and the amenity value (less native biodiversity, spiky seedheads are uncomfortable to hikers) of these Californian landscapes.

vices is scarce (see Díaz et al. 2005), and, to our knowledge, there is no published study explicitly addressing the effects of these mechanisms on global change drivers.

Resource use complementarity and facilitation are based on trait differences between species, i.e., their effects are expected to be maximal when species are very different from each other. Therefore, in those systems where these mechanisms indeed lead to enhanced ecosystem functioning, one should reasonably predict increased or decreased ecosystem 'performance' on the basis of an expanding or shrinking range of plant traits (Hooper 1998; Petchey 2003). However, there are other types of interactions that are both common and play an essential role in the preservation – or disruption – of ecosystem processes and services, and yet are not directly linked to the range of traits present in the local community. Major examples are interactions involving keystone species (Power et al. 1996), interactions involving ecosystem engineers (Jones et al. 1994), and indirect interactions (Box 7.2). 'Ecological surprises' in which the removal or introduction of species has triggered dramatic changes in ecosystem processes and services, often with very high cultural and economic costs, usually involve one or more of these types of interactions (see Díaz et al. 2005 for review and examples of 'ecological surprises'). In all these cases, changes in ecosystem processes and services, and feedbacks to global change drivers, are not easily predictable from species richness or from any of FD components (i.e., neither from the kind, or the relative abundance, or the range of traits present). The functional *identity* (*kind* of traits) of the introduced or removed species is of prime importance in determining these unexpected (and often negative) ecosystem-level impacts. Unlike in the mass-ratio hypothesis however, there is no easy a priori link between the traits of the species in question and putative ecosystem processes or feedbacks onto global change drivers. This represents one of the toughest challenges to the FD approach, and an extremely promising venue for new research.

7.4   Summary and Conclusions

Functional diversity (FD) comprises the *kind*, *range*, and *relative abundance* of functional traits present in a given community. Major global change drivers, including changes in climate, atmospheric composition, land-use/disturbance regime, and biotic exchanges, affect and are affected by FD in a non-random, and often predictable way. There is overwhelming evidence that the *kind* of traits that are present in higher abundance are major drivers of short-term ecosystem processes and their feedbacks onto global change drivers. Both the response of plant traits to environmental filters and their effects on biogeochemical and biophysical ecosystem processes (including simple, direct interactions with herbivores and decomposers) can be predicted with acceptable accuracy, although

present theory cannot account for the mutually-neutralizing or synergistic effects of combinations of traits.

The role of the *range* of traits in influencing ecosystem functioning by resource use complementarity and facilitation is less clear, and fewer empirical examples are available, although both theory and some experimental evidence suggest that the role of subordinate species is important in maintaining long-term stability. Finally, there are other biodiversity-related effects, which are the result of indirect interactions, and/or interactions involving keystone species and/or ecosystem engineers, that cannot be predicted on the basis of the kind, range or relative abundance of traits, and remain a major challenge for the FD approach.

Non-linearities that are triggered by changes in climate, land-use regime and/or biotic interactions that involve altered FD, and in turn affect global change drivers and ecosystem services, represent a major threat to the integrity of the life-support systems. There is therefore an urgent need for more theoretical and empirical studies that would lead to better understanding and anticipating their consequences.

The quantification of functional diversity is not free from difficulties, and it is certainly less straightforward than counting the number of species, at least in areas with well-described floras. However, it provides a much stronger insight into the links between community structure, ecosystem functioning, and global change drivers and ecosystem functioning than does the consideration of species richness alone. Major venues for future research in FD are (1) the identification of those functional traits or functional trait combinations that are more likely to trigger ecosystem and landscape-level non-linearities; (2) continued efforts to measure functional traits under a wide range of biomes and regions, following standardized lists and protocols (see Lavorel et al. 2007, Chap. 13 of this volume); (3) more empirical investigation on how important are the roles of resource use complementarity and facilitation in determining ecosystem functioning under different degrees of environmental filtering; (4) more empirical and theoretical work on how FD effects on ecosystem processes translate into changes in global change drivers and ecosystem services; and (5) the design of easily-workable FD indices that could be applied to a wide range of natural situations, and thus broaden the possibilities of empirically testing the functional role of biodiversity.

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