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Functional traits underlie the delivery of ecosystem services across different trophic levels

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Abstract

Functional traits of organisms can serve as tools for predicting and quantifying ecosystem service delivery in response to biodiversity loss. We collected published studies (~250) proving effects of functional traits on various ecosystem services, and the underlying ecosystem processes, across different trophic levels. The majority of studies considered plants and soil invertebrates, but relationships have been documented for a range of other organisms and habitats. Within each trophic level, specific processes and services are affected by a combination of traits. At the same time, particular traits are involved simultaneously in the control of different processes, resulting in predictable clusters of traits and services. Particular associations were shown between traits of plants and soil organisms that underlie ecosystem nutrient economy, herbivory control and fodder and fibre production. The review demonstrates the potential for integrating the functional traits approach into predictive models of ecosystem services and providing a common currency for multiple service delivery assessments.

Introduction

The recent emphasis on ecosystem services as a currency to value ecosystems and promote their sustainable use (Millennium Ecosystem Assessment 2005) has drawn attention to the way different organisms contribute to ecosystem service delivery (Luck et al. 2003; Kremen 2005; Díaz et al. 2007). Ecosystem service providers are species, functional groups, populations or communities that contribute to ecosystem service provision in a given system (Bengtsson 1998; Kremen 2005). A first step to ecosystem service assessment, therefore, consists of identifying which organisms contribute to those ecosystem properties that underlie ecosystem services of interest. This task has now been undertaken in several studies, which have identified the key roles of pollinators (see Kremen et al. 2007 for a review), particular plant groups as nitrogen fixers (Spehn et al. 2002), soil or sediment engineers (Wardle et al. 2004; Boyero et al. 2007), or soil microbial groups (Bailey et al. 2002; Heemsbergen et al. 2004).

To quantify the impact of biodiversity changes on ecosystem service delivery it is necessary to identify those characteristics and mechanisms by which organisms affect ecosystem properties (Eviner & Chapin 2003; Hooper et al. 2005; Kremen et al. 2007). Such an approach has been proposed for populations (i.e. single species), where demographic attributes (e.g. population density) may serve as indicators of service provision (Luck et al. 2003). In other cases however, ecosystem properties and services are controlled by the functional traits shared by several species in a given trophic level (Díaz & Cabido 2001; Eviner & Chapin 2003; Lavorel & Garnier 2002; Díaz et al 2007). This arises when particular groups of organisms with specific characteristics, for example the nitrogen-fixers or denitrifiers, drive ecosystem service provision. These groups need not have a taxonomic basis, and are traditionally referred to as 'functional groups', i.e. groups of species with a similar effect on ecosystem properties because of similar traits. Therefore group membership is determined by an organism's ecosystem effect, and also by a set of common characters, or functional traits, that can be associated with this effect (Lavorel et al. 1997; Box 1).

There is a growing consensus that the kind, range and relative abundance of functional traits in biotic communities, collectively referred to as 'functional diversity', strongly determine ecosystem processes (Díaz & Cabido 2001; Lavorel & Garnier 2002; Hooper et al. 2002; Eviner & Chapin 2003) and the delivery of ecosystem services (Millennium Ecosystem

Assessment 2005; Díaz et al. 2006, 2007; Petchey & Gaston 2006; Quétier et al. 2007). Despite the fact that biodiversity has often been equated only with species richness (i.e. number of species) and composition (Balvanera et al. 2006), there is now a growing number of studies linking ecosystem properties with functional diversity (Díaz et al. 2007). However, they have been scattered in the literature, with varying degrees of empirical support and varying functional diversity components analyzed (Díaz & Cabido 2001; Hooper et al. 2002; Eviner & Chapin 2003). Therefore, a first step towards the full use of functional diversity as a tool for predicting ecosystem service levels is the identification of those functional traits that underlie service delivery. In addition, very little is known about the relative role of different components of functional diversity, such as the dominant traits in a community or the range/functional divergence of traits (Box 1), on the delivery of ecosystem services (Díaz et al. 2007). A challenge for researchers is therefore to identify associations between ecosystem properties that contribute to ecosystem service delivery, and the various functional diversity components underlying these processes.

In this study, for the first time, we collected and organized the scattered information connecting the traits from different organisms (plants, insects and other invertebrates, microbes, etc.) to a variety of ecosystem processes and services. This exercise goes one step beyond previous reviews synthesizing the effects of biodiversity on ecosystem processes (Millennium Ecosystem Assessment 2005; Balvanera et al. 2006; Kremen et al. 2007) by considering explicitly which traits and functional diversity components relate to a range of services and analyzing this relationship in different organisms and habitats. Very little is known, in fact, about the extent to which functional diversity links the traits from different organisms to ecosystem services. Most studies have focussed on one particular trophic level (Díaz & Cabido 2001; Hooper et al. 2002; Eviner & Chapin 2003; Díaz et al. 2007; but see Wardle et al. 2004; Ortiz-Ceballos et al. 2007; Kremen et al. 2007) and considered one or a few services. Moreover, since traits are involved simultaneously in the control of different processes, our approach allows for the identification of clusters of associated traits and services (Balvenera et al. 2006). Such associations facilitate an understanding of the consequences of biodiversity management in a framework of multiple service demands (i.e. when multiple, sometimes conflicting, services are delivered by given biotic communities, e.g. productivity, soil protection and ecotourism demands; Hodgson et al. 2005; Quetiér et al. 2007). In this context, we asked the following questions:

(1) What is the empirical evidence for links between the functional traits of organisms and ecosystem service delivery?
(2) How is this knowledge spread across different types of organisms, habitats and categories of ecosystem services?
(3) Are there identifiable ‘bundles’ of ecosystem services, or service syndromes, that can be linked to a combination of functional traits?

Box 1. Terminology relating to the functional components of diversity

Functional trait
A characteristic of an organism, which has demonstrable links to the organism's function. As such, a functional trait determines the organism's response to pressures (*response trait*), and/or its effects on ecosystem processes or services (*effect trait*). Functional traits are considered as reflecting adaptations to variation in the physical and biotic environment and trade-offs (ecophysiological and/or evolutionary) among different functions within an organism. In plants, functional traits include morphological, ecophysiological, biochemical and regeneration traits, including demographic traits (at population level). In animals, these traits are combined with life-history and behavioural and feeding habit traits.

Functional attribute
The value of a functional trait. It may be categorical (e.g. C3 vs C4 for plant photosynthetic pathway) or quantitative.

Functional group
A group of species with similar suites of co-occurring functional attributes. Groups are traditionally associated with similar responses to pressures and/or effects on ecosystem processes. A functional group is often referred to as 'guild', especially when referring to animals, e.g. the feeding types of aquatic organisms having the same function within the trophic chain.

Functional diversity
The kind, range and relative abundance of functional attributes in a given community (Díaz & Cabido, 2001; Díaz et al., 2007). Functional diversity can be quantified by different components, for which the most important are the 'dominant traits in a community' and the 'functional divergence'.

First, the mass ratio hypothesis (Grime 1998) states that the traits of the dominant species in a community exert a key effect on several ecosystem processes. The dominant traits in a community can be estimated by different measures, such as the weighted trait mean value in a community (the average trait value in a community weighted by the relative abundance of the species carrying each value) or, simply, as the relative abundance of given functional groups (e.g., the abundance of nitrogen fixing species).

Second, functional divergence represents the degree of functional dissimilarity and complementarity in trait values within the community. This can be expressed through various metrics, including functional divergence (Mason et al. 2005; Leps et al. 2006) and the number of functional groups (i.e. functional richness: Díaz & Cabido 2001; Balvanera et al. 2005).

Methods

We collected and analyzed literature documenting links between functional traits and ecosystem services, and the underlying ecosystem processes, for a range of organisms and habitats. Our focus was on the functional dimension of biodiversity, therefore we did not consider studies simply assessing species diversity or species composition, while selecting only studies considering explicitly traits or functional groups of organisms. In the collection, moreover, only those studies with a mechanistic link between traits and ecosystem processes were selected, while excluding studies where the relationship was not clearly demonstrated.

In total, 247 references were included in the database (see Appendix). Each entry was classified based on 10 criteria: (1) whether the study was a review or presented an original data analysis; (2) the ecosystem service category assessed according to the Millennium Ecosystem Assessment (2003; 'provisioning', 'cultural' and 'regulating and supporting' services; the last two categories were considered together as one, see below); (3) the specific ecosystem service assessed; (4) the ecosystem process underlying the service; (5) at which level of organization the traits were considered (see details below and Box 1); (6) the specific traits considered; (7) whether traits were assessed in combination with other traits or were considered individually; (8) the relationship of traits with ecosystem processes and services (the increase in trait value/abundance improved, or was detrimental to the process, or the relationship was not identifiable); (9) the organisms providing the service; and (10) the ecosystem type in which the study was undertaken. In the resulting database, 548 entries (rows) were obtained, as studies assessing multiple traits, or processes/services, were defined by multiple rows (i.e. one for each trait and service combination).

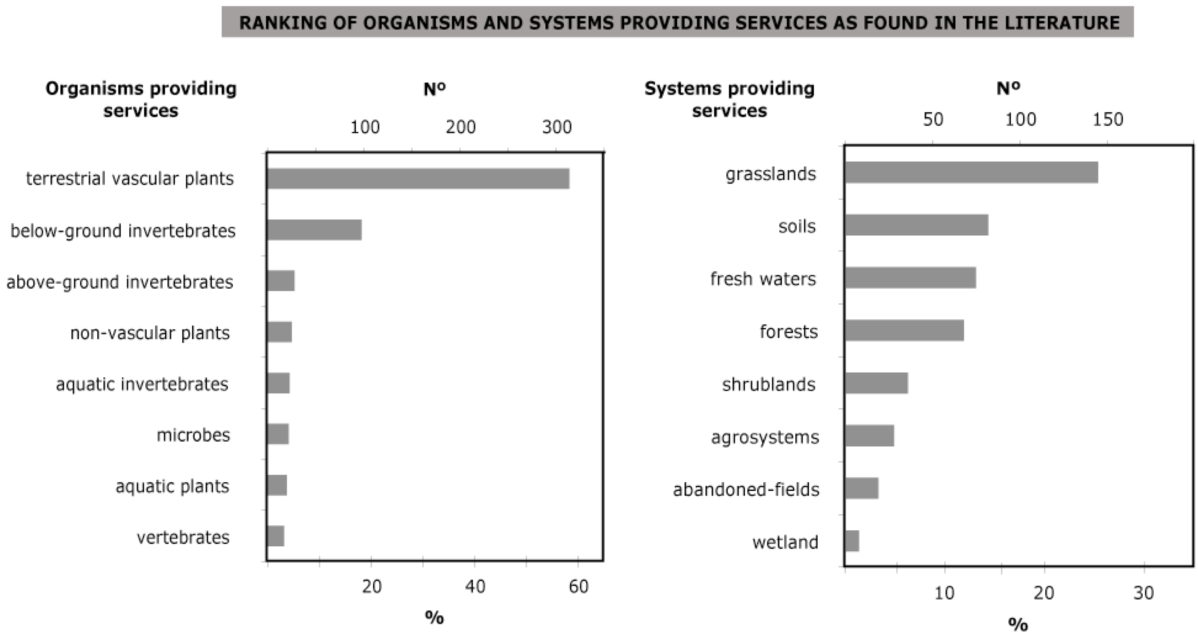
For the level of organization at which functional diversity was assessed (criterion 5 above) we distinguished studies (5a) at species level, i.e. species with different traits resulted in different ecosystem effects; (5b) at functional group level, i.e. different functional groups resulted in different ecosystem effects; (5c) at the level of the dominant traits in a community, i.e. communities with different dominant traits resulted in different ecosystem effects (Grime 1998; Díaz et al. 2007), (5d) at the level of range of traits in a community, which include indices of functional divergence (Mason et al. 2005; Leps et al. 2006) or functional group richness (Díaz & Cabido 2001; Hooper et al. 2005; Balvanera et al. 2006). These four categories were not exclusive, e.g. a study considering functional group richness would be introduced into the table as a case carried out at both functional group level and functional range level. In this review, we then grouped together the ecosystem services identified by the Millennium Ecosystem Assessment as 'regulating' and 'supporting' services because, in most cases, a clear objective distinction between the two categories was not possible. Ecological processes such as herbivory and seed dispersal, recognized elsewhere as ecosystem services (http://www.maweb.org/en/index.aspx), were considered as processes affecting several specific services (e.g., biocontrol, decomposition or food production).

The database was explored via number and frequency counts of the entries defined for the different criteria. Then, to identify bundles of traits and processes (Balvanera et al. 2006) we used a multivariate analysis approach (i.e. Detrended Correspondance Analyses, DCA, using CANOCO; ter Braak & Smilauer 1998). This technique was used to show the similarity among ecosystem processes in terms of the traits that predict them (for details on methods see Figure 4 caption). In the DCA, the association among services and traits was based on contingency tables (Chi-square) visually represented by distance between points in a multivariate space. Therefore, this approach allowed visualization of the degree of association between processes and different traits, as well as the overlap of associated traits effects on multiple processes.

Results

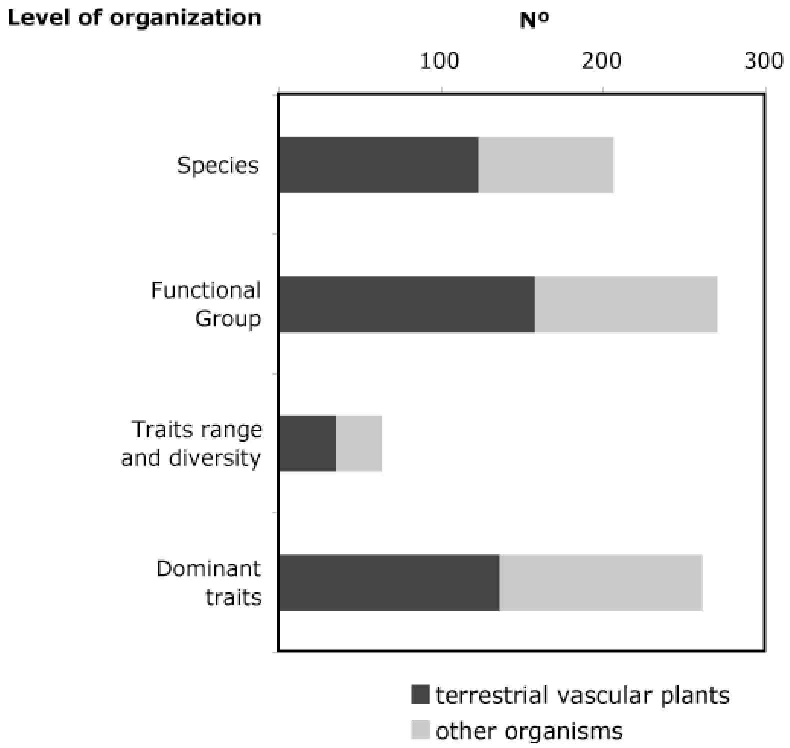
Relationships between traits and services have been documented for a range of organisms and environments. Most studies considered in the database focused on the effect of vascular plant (57% entries) and soil macrofauna traits (18%; Figure 1). The systems most frequently considered were semi-natural grasslands, forests and shrublands (altogether 45% of the entries), while a reasonable number of studies focused specifically on services delivered by soils (15%) or freshwater systems (14%; Figure 1). Functional trait effects on ecosystem services were most frequently reported at the levels of functional groups and the dominant traits in a community (Figure 2). To a lesser extent, the range of trait values present in a community played an important role (69 entries), especially in services based on primary productivity, nutrient cycling, pollination, and the maintenance of these services through time (i.e. stability and resilience).

Figure 1. Distribution of service-trait relationship information by organism and system type (number and percentage of entries in the database as found in the literature are shown - note each study recorded could generate more than one entry in the database, see methods). Entries (15%) not included in the system categorization (right figure) refer to meta-analyses studies.



Within organism types, a variety of traits has been reported to affect different ecosystem processes and services (Table 1). Effect traits (Box 1) considered referred mostly to the morphological and chemical structure of plants, and to feeding habit and substrate type for fauna and microbes. Morphological characteristics most frequently assessed in animals were body size or biomass (17 entries), relative growth rate (18) and tongue length or mandibular structure (2). All other effect traits considered in animals were behavioural (nesting activity, mobility, environmental and temporal niche range etc.). Several key traits appear to influence simultaneously a range of ecosystem services (Table 2), for example leaf chemistry and morphology, canopy and root architecture in plants, and body size and feeding habit in soil invertebrates. While the services affected by these traits often coincide, the degree of relevance (i.e. number of entries) for each trait per service varied. For example, leaf and canopy traits both affected services related to fertility and nutrient cycling and the regulation of water and climate. However, leaf traits affected more frequently those services acting at smaller scales (i.e. local fertility) whilst larger scale services were more strongly affected by canopy traits (water and climate regulation).

Figure 2. Levels at which the collected studies assessed the relationship between traits and ecosystem services (see methods and Box 1 for details).



Overall, most processes for which trait effects have been documented can be classified into "regulating and supporting" services (Millennium Ecosystem Assessment 2005). The processes most often affected by traits were decomposition and mineralization, nutrient retention and sedimentation, productivity for fodder and fibre, evapotranspiration and herbivory control (Figure 3). A clear mathematical relationship between trait composition and the delivery of services (either a positive or detrimental effect of given traits) could be established in most cases considered (69%). In particular, the increase in traits value/abundance improved services in 50% of the entries and it was detrimental in 19% of the entries, while the relationship was more complex in the remaining ones (i.e. studies demonstrated effects of functional traits composition without specifying in which specific way traits, or functional groups, affected the linked processes).

Table 1. Traits considered in the literature for the different organisms. Numbers in parentheses indicate the number of entries in the database.

organism group	organisms	traits	nº
vascular plants (311)	plants (311)	canopy size/architecture	33
		flammability	2
		flower traits	15
		growth form	105

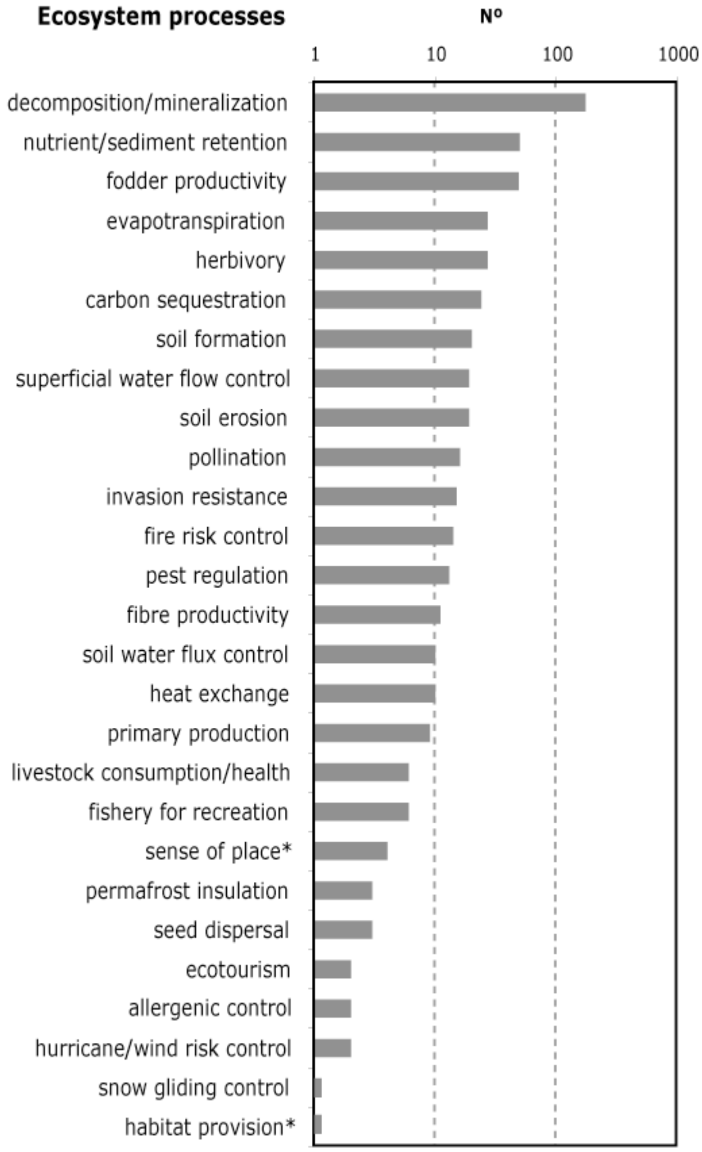
organism group	organisms	traits	nº
		leaf chemistry	16
		leaf morphology	40
		litter abundance/chemistry	7
		mycorrhization	1
		nitrogen fixing	12
		parasitic capacity	2
		phenology	7
		photosynthetic traits	6
		root chemistry	4
		root size/complexity	18
		tissue chemistry/compounds	43
non-vascular plants (29)	lichens (4)	organic acids	2
		chlorophyll content	1
		growth form	1
	bryophytes (22)	cation exchange	1
		growth form/biomass	6
		host of nitrogen fixing bacteria	1
		litter quality	3
		desiccation tolerance, lack of cuticles, low thermal conductance	16
	lichens & bryophytes (3)	-	
aquatic plants (20)	macrophytes (19)	floating type/growth form	6
		relative growth rate	5
		reproduction type	1
		root oxygen loss	1
		root:shoot	3
		size/space occupancy	2
		specific leaf area	1
	algae (1)	lack of roots, stem, vascular tissues	1
aquatic invertebrates (23)	benthic fauna (4)	feeding habit	4
	caddisflies (1)	feeding habit	1
	chironomids (2)	feeding habit	2
	crustaceae (1)	feeding habit	1
	decapods (1)	feeding habit	1
	mussels (3)	biomass	2
		excretion rate	1
	shredders (6)	bioturbation potential	5
		temporal niche	1
	snail (5)	feeding habit	5
microbes (22)	bacteria (3)	substrate type	3
	fungi (7)	entomopathogens	4
		substrate type	3
	bacteria & fungi (10)	relative growth rate	1
		substrate type	9
soil invertebrates (98)	ants (8)	foraging at low tº and disturbed sites	1
		nesting type, amount of soil moved	6
		specialization	1
	arthropods (2)	feeding habit	2
	collembola (11)	feeding habit	8
		relative growth rate	3
	detrivore groups (19)	feeding habit	16
		life history	3
	earthworms (29)	body size	3
		feeding habit	25
		relative growth rate	1
	enchytraeids (7)	feeding habit	7

organism group	organisms	traits	nº
	millepedes (1)	feeding habit	1
	shredders (1)	feeding habit	1
	termites (5)	burrowing activity	5
	macrofauna (14)	body size	9
		feeding habit	6
above ground invertebrates (28)	pollinators (8)	body size	2
		generalists/specialists	2
		tongue length	1
		morphometry	1
		FD	2
	beetles (2)	dung exploitation, size and diel activity	2
	pathogenic earthworms (6)	virulence, survival and mobility	3
		fitness of symbiotic bacteria, heat/desiccation tolerance, reproductive capacity	3
	ladybirds (1)	feeding specificity, voltinism, size, mandibular structure	1
	hoverflies (2)	migratory status, feeding habit	2
	aphids (3)	polyphagy, starvation capacity, mobility	3
	insects (5)	feeding habit	2
		generalists/specialists	2
	predators (2)	feeding specificity, life cycle	2
vertebrates (17)	beavers (6)	building capacity	6
	fish (11)	relative growth rate	4
		feeding habit	7

Table 2. Most common plant and invertebrate traits and their involvement in ecosystem services delivery. Services linked to each trait group are ordered from more to fewer entries in the data base. * = body size can be related to feeding habit.

organisms	Traits	services (from more to less entries)
terrestrial plants	leaf nitrogen content	fertility and nutrient circulation, biocontrol, fodder production, sense of place
	leaf dry matter content	fertility and nutrient circulation, fodder production, biocontrol, natural and hazard control
	canopy architecture	climate regulation, water regulation, soil stability and formation, fibre production, natural hazard control, fertility and nutrient circulation, habitat provisioning
	root architecture	water regulation, soil stability and formation, fertility and nutrient circulation, climate regulation, fodder production
soil invertebrates	body size*	fertility and nutrient circulation, soil stability and formation, water regulation, climate regulation, habitat provisioning

Figure 3. Distribution of service-trait relationship information by ecosystem processes assessed. Log-scaled number of entries in the data base. * = cultural services not directly underlined by a single ecosystem process.



A combination of several traits within each trophic level contributes to the delivery of a given service. For example evapotranspiration processes are modulated simultaneously by various plant traits (canopy density, canopy size, leaf area, leaf dry matter content, phenology, root depth, growth form, stomatal conductance; see Appendix). In addition, various organisms and their traits are shown to be involved simultaneously in ecosystem service delivery (see Appendix). Despite this, fewer than half the cases found in the literature considered the possible combined effect of various traits on ecosystem service delivery (45.4%) and only 2% considered more than one trophic level (mostly plants together with pollinators or soil invertebraes/microbes).

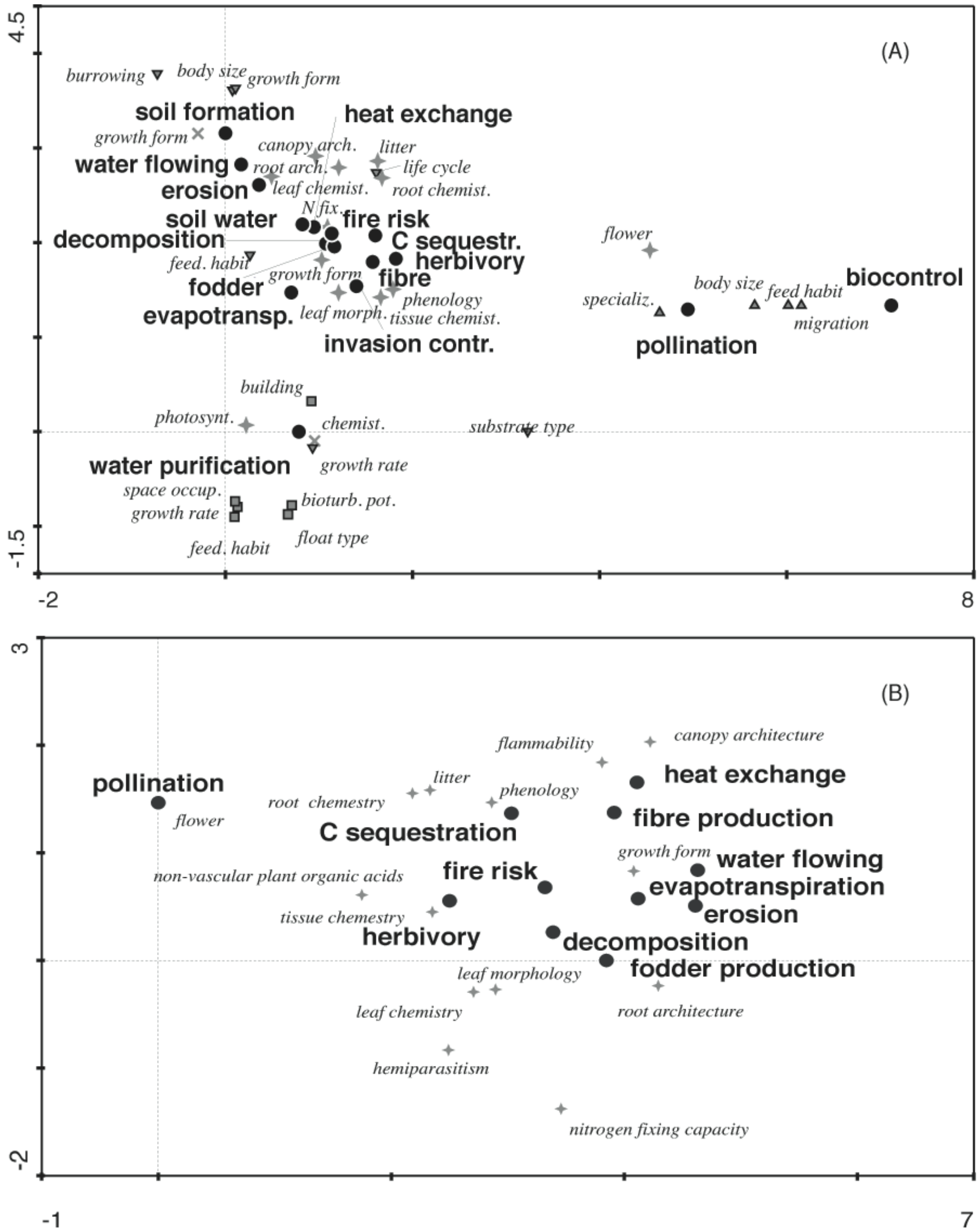
The involvement of a given trait in multiple service delivery (Table 2) and the dependence of each service on a range of traits (Appendix) result in clumps of associated traits and services (Figure 4). In particular, the DCA analysis considering all main organisms, and processes from the database (Figure 4A) was strongly driven by differences in the specific functions associated with different types or organisms. This complete analysis (first two DCA axes accounting for 39% of variance; first axis 25%) discriminates the pollination and biocontrol services provided by insects (right hand side of Figure 4A), from the water purification service mediated by a range of aquatic organisms (bottom left) and a third, much larger, cluster of functions and associated services (top left). This cluster is mediated by a range of plant and soil organisms and shows close associations among those traits that underlie, for example, ecosystem nutrient economy (through effects on carbon sequestration, decomposition), herbivory control, productivity (provided mostly by different plant traits) and the services related to water flow and soil formation (provided mostly by soil invertebrate traits). As these main clusters are to some extent intuitive, and the large cluster involves a wide range of organisms, it appears logical to run a separate analysis involving just plants, which have by far the largest number of entries in the database (Figure 1). This analysis (Figure 4B; first two DCA axes accounting for 43% of variance; first axis, 28%) confirms the previous results but improves the visual clarity of the association between plant traits and the processes and services to which they contribute. In particualar, a common set of traits was associated to processes such C sequestration, herbivory and fire risk (in a central cluster in the graph).

Discussion

The review shows that the functional components of diversity are key constituents of biodiversity, underlying a range of ecosystem services across different trophic levels and habitats. The compilation of this database allows a review of knowledge on the links between functional traits and ecosystem service delivery. In particular, the study evidences how the combined effect of various traits is exerted on bundles of associated ecosystem services.

Within each trophic level, specific processes and services are affected by a combination of traits (Table 2, Figure 4 and Appendix). While this has been previously suggested for plants (Eviner & Chapin 2003; Díaz et al. 2007), we have shown here specific associations between processes affected by common sets of trait as well as the overlap of traits effects on different processes. For example, particularly clear associations were found between those traits of plants that underlie ecosystem nutrient economy, herbivory control and fodder and fibre production. Such associations can provide a common currency for managing multiple, and often conflicting, service requirements from the landscape (Quétier et al. 2007). For example, a trait configuration that improves fodder production will be likely to have consequences for carbon sequestration (Figure 4; Wardle et al. 2004; Dijkstra et al. 2006) but might be detrimental to services linked to aesthetic and cultural values (Appendix; Hodgson et al. 2005; Quétier et al. 2007). Therefore the management of functional diversity for given service delivery should take into account possible positive or negative feedbacks on the associated services.

Figure 4. Association between traits and ecosystem processes (A, including all organisms; B, only plants, i.e. vascular and non-vascular). The DCAs show the similarity among ecosystem processes (black circles) in terms of the traits (different symbols for different organisms) that predict them (distance between two points reflects contingency). For this, processes were considered as dependent variables defined by different traits (i.e. processes were considered ‘samples’ and traits as ‘species’ in the analyses). Only those processes with more than ten entries in the database (see Appendix) were considered. The number of times different groups of traits affected given processes were log(x+ 1) transformed prior to analysis and the ‘downweighting of rare species’ option in CANOCO (for details see Leps & Smilauer 2003), i.e. to minimize the differences in the number of traits considered per process while keeping infrequent traits from having a strong influence on the analyses. Traits observed are those which showed a higher weight in the DCA analyses. The first two DCA axes, accounting around 40% variance for each analysis, are shown. Symbols are: “star” for vascular plants, “cross” for non-vascular plants (only in A), “downward-triangle” for below-ground invertebrates “upward-triangle” for above-ground invertebrates, “quadrate” for all different aquatic organisms.



The review highlights also that, while a given trait can contribute simultaneously to the control of different processes (Appendix), the extent of these associations depends on the range of spatial scales at which the effect trait operates and in relation to the spatial scale at which the services are delivered (Table 2). For example, strong control of fertility and nutrient circulation by leaf traits has been demonstrated repeatedly (Table 2; Garnier et al. 2004; Wardle et al. 2004; Hodgson et al. 2005) while canopy trait effects are exerted most noticeably on climate and water regulation (Eviner & Chapin 2003; Chave et al. 2005; Díaz et al. 2006). Therefore, while relatively few key traits can control different services and processes, their relative importance needs to be considered depending on the spatial scale at which the ecosystem services operate.

Another, more obvious, pattern shown by the analyses of the database is that different processes and services are usually associated with different types of organisms. For example services mediated mostly by plant and soil organisms are discriminated from those provided by aquatic organisms and those provided by above-ground insects (Appendix; Figure 4A). Even if we show here that ecosystem processes are not likely to be affected only by single trophic levels (Appendix; Wardle et al. 2004; Kremen et al. 2007), the database and multivariate approach presented can offer a tool to operate a screen of organisms whose traits are more important for the given ecosystem services under assessment.

Most of the proven links between functional diversity and ecosystem services in the literature are reported in systems with complex biotic assemblages. The large number of studies for these systems, and particularly those considering plant traits in grasslands, shrublands and forests (Figure 1), probably reflects the fact the functional traits approach has had more recent development in plant species-rich communities (e.g. McIntyre et al. 1999). In these systems the functional approach has been advocated especially to deal with the impossibility of considering each taxonomic entity separately, and thus attain a system simplification (Lavorel et al. 1997; Díaz et al. 2007). Similarly, in soil and fresh water systems, the functional approach has been applied to simplify their complex trophic structures and their effect on ecosystem processes (Bradford et al. 2002; Mehner et al. 2002; Nannipieri et al. 2003).

This review indicates also that there is no particular reason to limit the functional approach to particular types of organism and to more simple systems, while taking into account that the trait approach can be tailored to specific contexts. For example, trait types are obviously different among organisms. This is because, despite the fact that the main axes of trait differentiation are generally the same (food, regeneration, space), the resources and resource acquisition strategies are different for different organisms types (Díaz et al. 2004; Cole et al. 2006; Kremen et al. 2007). Thus, trait links to ecosystem services reported in the literature are based mostly on structural traits in plants and on behavioural traits in animals. The search for easily measurable structural traits has been pursued with plants. Therefore, while shortlists of key traits and standardized protocols have been available for some time in the case of plants (Cornelissen et al. 2003), similar standardizations are still underdeveloped for other organism types. Soil organisms (including microbes), or aquatic invertebrates are often classified according to their substrate type and/or their habitat (e.g. soil depth for earthworms), which amounts to considering their ecosystem effects as a primary key for classification (Heemsbergen et al. 2004). Recent development, however, points towards the consideration of more structural traits, such as body size and digestive apparatus, especially in invertebrates (Bradford et al. 2002; Kremen et al. 2007; de Bello et al. 2007), as a way to identify easy measurable effect traits.

Most processes for which published evidence exists that they are affected by traits can be classified within the "regulating and supporting" Millennium Ecosystem Assessment services categorization. Provisioning services, mostly delivered by agroecosystems, have been assessed so far to a much lesser extent from the functional diversity point of view (Appendix and Figure 1). While it is known that provisioning of food, biochemicals and natural medicines relies on the particular traits of selected species (which is also the main tool and criterion of, for example, agronomic selection) provisioning services depend often on the traits of particular species (e.g., monocultures) or on habitat attributes, resulting in a minor interest in the functional diversity approach. Notable exceptions are the provisioning of fodder and fibre and the delivery of freshwater, traditionally based on multispecies assemblages, for which we found several studies documenting trait effects on the underlying ecosystem processes (Appendix and Figure 1). Similarly, cultural services have been traditionally linked to particular habitats and species of conservation value, resulting in a lower interest in the functional traits approach. Nevertheless cultural services, such as ecotourism are also mediated by species traits, for example the abundance and diversity of floral type, flower colour and phenology (Turpie & Joubert 2004; Quétier et al. 2007).

Our database, furthermore, indicates that a simple mathematical relationship between traits and services is often identifiable (Figure 4). This shows that direct quantification of ecosystem service delivery based on the assessment of trait composition in biotic communities can be established for practical purposes. This approach has a particular potential for future research and applied management, as shown by the few recent studies demonstrating direct service quantification via functional traits (Hodgson et al. 2005; Quétier et al. 2007). In this context, the functional traits approach needs to be considered as another important tool for predictive models of ecosystem service delivery, together with more taxonomical approaches, i.e. those based on species richness and species composition/identity (Luck et al. 2003; Balvanera et al. 2007). Further, ecosystem process regulation depends, to a great extent, on abiotic controls (Díaz et al. 2007), on the population of key species (Luck et al. 2003) and on the combination of several traits (Eviner & Chapin 2003). Available frameworks, therefore, need to integrate these different factors to produce an applied tool for service assessment (Díaz et al. 2007). Given that ecosystem processes and services rely on organisms from different trophic levels (Millennium Ecosystem Assessment 2005; Appendix), the match between traits and services will certainly benefit from further consideration of interactions among different trophic levels, i.e. top down and bottom up effects.

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Appendix. Species and traits relating to different ecosystem services (categories modified from Millenium Ecosystem Assessment 2005) and underlying processes. *** Herbivory and seed dispersal can affect several services, see methods.

MEA cat.	services	processes	organisms	traits
regulating & supporting (458)	water regulation (56)	evapotranspiration (27)	terr. vasc. plants (22)	canopy density, canopy size, leaf area, leaf dry matter content, phenology, root depth, growth form, stomatal conductance
			bryophytes (1)	desiccation tolerance, lack of cuticles, low thermal conductance
			macrophytes (4)	submerged vs floating, RGR, size
		soil water fluxes (10)	terr. vasc. plants (6)	growth form composition, canopy size/density, litter biomass
			earthworms (3)	feeding habit (endogeic, anecic, and epigeic), body size
			beavers (1)	building capacity
		surface water flow (19)	ants (3)	nesting type, amount of soil moved
			beavers (1)	building behaviour
			bryophytes (1)	biomass
			earthworms (5)	size, soil position/feeding habit (endogeic, anecic, and epigeic)
			termites (4)	burrowing activity
			terr. vasc. plants (5)	growth form, life cycle, canopy size/architecture
	water purification (50)	nutrient/sediment retention/water transparency (45)	microbes (4)	RGR, carbon uptake strategy, substrate type (e.g. cellulositic, nitrifiers)
			beaver (1)	building capacity
			bryophytes (1)	litter quality (N content, cation exchange, phenolics)
			benthic fauna (11)	feeding habit and bioturbation potential (shredders, chironomids, decapods, caddisflies)
			fish (6)	feeding habits (e.g. piscivores/zooplanktivores)
			macrophytes (11)	submerged vs floating, RGR, size, oxygen loss, SLA
			mussels (1)	body size
			snail (2)	feeding habit (plant/detritus/algae)
			terr. vasc. plants (6)	growth form (e.g. grasses), decomposability, leaf area, transpiration rate
			beavers (1)	building behaviour
			algae (1)	root and vascular system
		oxygen regulation in water (5)	snails (3)	feeding habit (plant/detritus/algae)
			benthic fauna (2)	bioturbation potential

MEA cat.	services	processes	organisms	traits
	soil stabiltiy and water run-off (22)	erosion (19)	bryophytes and lichens (4)	lack of roots, desiccation tolerance
			detritivores (7)	detritivore feeding habit (collembola, earthworms, enchytraeis, millipedes)
			terr. vasc. plants (8)	growth form (i.e. grasses and woody species), root depth/density, canopy size and architecture
		permafrost insulation (3)	vasc. and non vasc. plants (3)	growth form (e.g. herbs vs mosses), thermal conductance, canopy size and architecture
	soil formation (21)	soil formation (21)	soil macrofauna (14)	earthworm abundance and size/soil position, enchytraeids and termite abundance and ant abundance
			terr. vasc. plants (6)	growth form compositon, lignin, root litter quality and quantity, root size and complexity
			lichens (1)	organic acid production
	fertility and nutrient cycling (177)	nutrient mobilization, microbial activity, decomposition & mineralization (177)	detritivores and soil macrofauna (58)	substrate type, body size, collembola RGR, dissimilarity in effects on soil, ecomorphology (collembola, microarthopods, earthworms, enchytraeids)
			bryophytes and lichens (6)	host of nitrogen fixing bacteria and non vascular plant abundance, desiccation tolerance, low thermal conductance
			ants (2)	ant specialization, burrowing activity
			microbes (8)	substrate type (e.g. cellulolytic)
			terr. vasc. plants (98)	N fixing capacity, growth form, hairy root clusters, terpene content, root organic acids, fine root length, time of flowering, biomass:N, root organic acids, litter biomass, leaf traits (N, LDMC, toughness, lignin, SLA, Ca+), labile C, tissue chemistry (C:N, lignin), presence of arbuscular mycorrhizal fungi
			macrophytes (1)	macrophyte growth form
			benthic fauna (1)	feeding habit
			mussels (1)	excretion rate
			hemiparas. plants (1)	parasitic capacity/status
	natural hazard protection (15)	snow gliding risk (1)	terr. vasc. plants	leaf tensile strength, growth form
		hurricanes/wind damage control(2)	terr. vasc. plants	growth form (i.e. woody species), root depth
		fire risk (12)	terr. vasc. plants	resin, terpene and oils content, self pruning/ramification, twig/leaf dry matter content and area, growth form (resprouters and grasses proportion), flammability
	climate regulation (39)	heat exchange (10)	terr. vasc. & non vasc. plants	canopy size/complexity, growth form, leaf phenology, photosynthetic rate

MEA cat.	services	processes	organisms	traits
		carbon sequestration in plant and soil (29)	microbes (3)	substrate type (e.g. cellulolytic)
			detrivores (3)	substrate type and life history
			terr. vasc. plants (20)	canopy size and architecture (e.g. trunk diameter, wood density), tissue N, litter biomass, time flowering and seed output, root size and nutrients, leaf phenology, photosynthetic rate, growth form
			bryophytes (1)	poikilohydry, desiccation tolerance, lack of cuticles
	disease control (2)	allergenic control (2)	terr. vasc. plants	pollen proteolytic enzymes, furocoumarin content
	biocontrol (44)	pest regulation (17)	earthworms (6)	virulence, survival, mobility, desiccation tolerance, fitness to symbiotic bacteria, reproductive capacity
			aphids(3)	polyphagy, mobility, starvation capacity
			fungi (4)	virulence, fecundity and reproduction time, heat/desiccation tolerance, dispersal ability
			insects (4)	predators feeding habit, migratory status, voltinism, body size
		herbivory*** (27)	plants (24)	tissue chemistry (N, phenolics tannins, terpenes, lignin, fibre), leaf morphology (toughness, trichomes, SLA, tensile strength, weight ratio), life history (phenology, ruderality)
			lichens (1)	organic acid
			soil macrofauna (1)	body size
			insects (1)	guild predators
	invasion resistence (15)	persistence and resistance of habitat and processes (15)	bacteria (1)	substrate type
			terr. vasc. plants (13)	N fixing, growth form (grasses, ruderality), phenology
			insects (1)	feeding habit
	pollination (16)	pollination (9)	invertebrates (9)	body size/morphometry, forage range, tongue length, feeding habit, migratory status
		pollinator provision (7)	plants (7)	flower traits (accessibility, attractiveness, density, abundance, nectar energy)
	habitat provision (1)	plant succession (1)	soil macrofauna	feeding guild

MAE cat.	service	process	organisms	traits
provisioning (78)	fodder (55)	accumulation of standing biomass (49)	terr. vasc. plants	canopy size, leaf traits (SLA, size, LDMC, N content, toughness), biomass:N, growth form (e.g. legumes), root density
		consumption and health of livestock (6)	terr. vasc. plants	tannins and N content, diversity in the chemical compounds
	fibre (11)	accumulation of standing biomass (11)	terr. vasc. plants (9)	canopy size and complexity, trunk diameter, wood density, growth form composition
			insects (1)	specialist/generalist
			beavers (1)	building behaviour
	primary production (12)	accumulation of standing biomass (9)	bryophytes and lichens (3)	abundance of non vascular plants, lichens chlorophyll A content
			earthworms (2)	earthworm abundance
			macrophytes (2)	macrophyte growth form
			microbes (2)	microbe substrate type
		seed dispersal*** (3)	ants (1)	foraging at low tº and disturbed sites
			beetles (2)	dung exploitation, size and diel activity
cultural (12)	recreation (6)	fishery (6)	fish (4)	relative growth rate
			beavers (1)	building behaviour
			plants (1)	growth form composition
		ecotourism (2)	plants (2)	flower type, number and size
	aesthetic values, cultural and sense of place (6)	accumulation of standing biomass and species coexistence (4)	plants (4)	leaf morphology and chemistry