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Linkages between biodiversity attributes and ecosystem services: A systematic review

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ABSTRACT

A systematic literature review was undertaken to analyse the linkages between different biodiversity attributes and 11 ecosystem services. The majority of relationships between attributes and ecosystem services cited in the 530 studies were positive. For example, the services of water quality regulation, water flow regulation, mass flow regulation and landscape aesthetics were improved by increases in community and habitat area. Functional traits, such as richness and diversity, also displayed a predominantly positive relationship across the services, most commonly discussed for atmospheric regulation, pest regulation and pollination. A number of studies also discussed a positive correlation with stand age, particularly for atmospheric regulation. Species level traits were found to benefit a number of ecosystem services, with species abundance being particularly important for pest regulation, pollination and recreation, and species richness for timber production and freshwater fishing. Instances of biodiversity negatively affecting the examined ecosystem services were few in number for all ecosystem services, except freshwater provision. The review showed that ecosystem services are generated from numerous interactions occurring in complex systems. However, improving understanding of at least some of the key relationships between biodiversity and service provision will help guide effective management and protection strategies.

1. Introduction

The significance and value of ecosystem services for human well-being is well known (e.g. Butler and Oluoch-Kosura, 2006; Costanza et al., 1997; Daily, 1997; de Groot et al., 2002; Harrison et al., 2010). Ecosystems provide four types of service: provisioning (e.g. food), regulating (e.g. water quality regulation and pollination), cultural (e.g. recreation) and supporting (e.g. nutrient cycling) (Millennium Ecosystem Assessment, MA, 2005). The importance of biodiversity in underpinning the delivery of both ecosystem services and the ecosystem processes that underlie them is well recognised (Díaz et al., 2006; MA, 2005), and our understanding of the nature of the biodiversity–ecosystem services relationship and the possible effects of biodiversity loss on the delivery of ecosystem services is increasing

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(e.g. Balvanera et al., 2006; Cardinale et al., 2006). Consequently, there is an increasing trend to integrate ecosystem service arguments within the management plans and strategies of protected areas (e.g. García-Mora and Montes, 2011), as well as the wider landscape (e.g. The Scottish Land Use Strategy, Scottish Government, 2011). However, ecosystem service-related argumentation is not undisputed (Schroter et al., 2014).

Early work on the biodiversity–ecosystem services relationship explored the contribution of habitats to different ecosystem services (Chan et al., 2006) and of individual species to the functional structure of ecosystems, as well as the impact of interactions, both between species, and between species and the environment, on ecosystem function (Balvanera et al., 2005). The link between ecosystem services and biodiversity has further been examined, not only in terms of species, but also genotypes, populations, species functional groups and traits in an ecosystem (Díaz et al., 2006).

Much recent work has focused on functional relationships between biodiversity and ecosystem services. Functional diversity is one of the most important biodiversity attributes affecting ecosystem services by impacting the underlying ecosystem processes (e.g. de Bello et al., 2010; Díaz et al., 2006). Research has focused on single species (Luck et al., 2009) and groups of species (Díaz et al., 2007; Hooper et al., 2005), in addition to a number of broader scale syntheses (e.g. Conti and Diaz, 2013). Other studies have tended to examine a small selection or individual ecosystem services (Kremen, 2005; Luck et al., 2009; Seppelt et al., 2011), with few spanning multiple ecosystems (Bastian, 2013; Lavorel and Grigulis, 2012). Trait[3] analysis (e.g. Balvanera et al., 2006; de Bello et al., 2010; Díaz et al., 2006; Hooper et al., 2005; Lavorel and Grigulis, 2012; Luck et al. 2012) has been shown to be useful in identifying specific links between species, ecosystem processes and ecosystem service delivery and can demonstrate the complexity of processes and interactions which occur in ecosystems (Fagan, et al., 2008; Gaston, 2000; Lavorel, 2013).

Population dynamics are another factor impacting ecosystem functioning and service provision. This was first highlighted by Luck et al. (2003), who proposed the concept of a Service Providing Unit (SPU) to describe the ecological unit which provides the ecosystem service. Subsequently, Kremen (2005) suggested identifying Ecosystem Service Providers (ESP) and the concepts were combined into the SPU–ESP continuum by Luck et al. (2009), showing how the ESP concept can be applied at various levels, for example population, functional group and community scales.

Knowledge on the links between biodiversity and the provision of ecosystem services is key for furthering arguments for ecological restoration (Rey Benayas et al., 2009; Bullock et al., 2011). It could also contribute to the management of protected and restored areas (Bastian, 2013) in order to meet the dual goal of optimising the delivery of ecosystem services and supporting biodiversity conservation (Palomo et al., 2014). However, despite a number of meta-analyses, and advances in research and understanding of this relationship (Balvanera et al., 2006; Bastian, 2013; Cardinale et al., 2006, 2012; Hooper et al., 2005; Luck et al., 2009; Mace et al., 2012) there remains much uncertainty over the effect of the complexity of biodiversity components on the ecosystem functioning that underlies service provision (Balvanera et al., 2014; Schroter et al., 2014). Current knowledge has been poorly integrated and few studies incorporate a wide range of both biodiversity attributes and ecosystem services. Also there are few studies using empirical evidence to examine the role of biodiversity in providing ecosystem services (Mertz et al., 2007), and the quantitative relationships between components of biodiversity and ecosystem services are still poorly understood (Carpenter et al., 2009; de Groot et al., 2010).

This review builds on current state-of-the-art concepts that link ecosystem service provision with biodiversity, particularly on the identification of ESPs. It examines the underpinning role of biodiversity for a range of ecosystem services from the provisioning, regulating and cultural categories (MA, 2005; CICES, Haines-Young and Potschin, 2013). We focus on the key biotic and abiotic attributes of individual ESPs and evidence of their influence on the delivery of particular services. We explore the direction (positive, negative or unclear) and strength (from very weak to very strong) of this influence in order to understand the multifaceted nature of the ESP-attributes-services relationships and indicate future research challenges. Our overall objective is to contribute to the understanding of the possible effects of biodiversity on ecosystem services and human well-being using network diagrams as an innovative approach to illustrate the complexity of interconnections. This also improves the scientific knowledge base allowing those biodiversity attributes that are crucial for the delivery of ecosystem services to be more effectively targeted in management plans. Importantly, unlike other similar studies, this review also documents possible negative effects of biodiversity on ecosystem service provision.

2. Material and methods

2.1. Data collection

Eleven ecosystem services were included in the review chosen to represent the key groups of services from the MA and CICES classifications (Table 1). In order to review and consolidate existing research on the linkages between biodiversity and these 11 ecosystem services, a literature search was conducted between July 2012 and August 2013 using Web of Science or Web of Knowledge. The primary aim of focusing on peer-reviewed academic literature was to find the best available knowledge reported by the scientific community. A systematic methodology was adopted in order to ensure that a rigorous and repeatable method was applied to each ecosystem service. The method consisted of three stages: (i) the generation of keywords, (ii) a systematic search, and (iii) extraction of the data.

Keywords were generated based on the results of a pilot test (conducted from February to April 2012) which showed that 'ecosystem services' is a relatively new term and, hence, only using this term in a literature search is likely to miss relevant papers. Thus, keywords specific to each ecosystem service were selected, accompanied by appropriate biodiversity terms which could be related to the given ecosystem service. We included both synonyms (i.e. the service) and antonyms (i.e. the disservice) in the search terms to enable negative, as well as positive, impacts of biodiversity on ecosystem service supply to be captured. Additional service-related terms were used if necessary to refine results when large numbers of papers were found for the initial search terms (see Online resources for a full list of search terms).

The objective was to find 50 relevant papers for each service in order to have a wide range of relationships and studies. For many ecosystem services, however, the number of relevant results using the above methodology was too few. In these cases, additional intelligent search approaches were utilised. These included: (i) searching the reference lists of relevant articles for secondary references which may be of interest (termed snowballing) and (ii) searching for papers that have cited the relevant papers (termed reverse snowballing). In total, 50 papers were found for all services except timber production and freshwater fishing, where only 35 and 45 papers could be found, respectively, after applying all search approaches. This reflects the

[3] Specific properties of species which define their ecological function and govern their impact on ecosystem processes and services (De Bello et al., 2010; Diaz and Cabido, 2001).

Table 1
The 11 ecosystem services included in the literature review and their association with the MA and CICES classifications.

Ecosystem service	MA classification	CICES division/group
Provisioning services:		
Timber production	Fibre (timber and wood fuel)	Materials/biomass (timber)
Freshwater fishing	Food (capture fisheries and aquaculture)	Nutrition/biomass (freshwater fish and marine fish)
Freshwater provision (quantity)	Freshwater	Nutrition/water
Regulating services:		
Water purification (quality)	Water purification/waste treatment	Mediation of waste, toxics and other nuisances/mediation by biotic and ecosystems
Water flow regulation (flood protection)	Natural hazard regulation	Mediation of flows/liquid flows
Mass flow regulation (erosion protection)	Erosion regulation	Mediation of flows/mass flows
Atmospheric regulation (carbon sequestration)	Climate regulation	Maintenance of physical, chemical, biological conditions/atmospheric composition and climate regulation
Pest regulation	Biological control	Maintenance of physical, chemical, biological conditions/pest and disease control
Pollination	Pollination	Maintenance of physical, chemical, biological conditions/lifecycle maintenance, habitat and gene pool protection (pollination)
Cultural services:		
Recreation (species-based)	Recreation and ecotourism	Physical and intellectual interactions with biota, ecosystems, and land-/seascapes/physical and experiential interactions
Landscape aesthetics	Aesthetic values	Physical and intellectual interactions with biota, ecosystems, and land-/seascapes/intellectual and representative interactions (aesthetic)

limited number of studies that have examined how biodiversity influences timber and fish production, despite the large amount of literature on the impact of best management and/or harvesting practices on wood yield/quality and the impact of fishing on fish attributes.

Data from the 530 papers were extracted into a database, with parameters covering: (i) the ecosystem service; (ii) the reference; (iii) the location of the study; (iv) the spatial scale; (v) the temporal scale; (vi) the ESP[4], (vii) the important biotic attributes of the ESP; and (viii) abiotic factors which affect service delivery. ESPs were categorised into seven groups: single population; two or more populations; single functional group; two or more functional groups; dominant community; single community/habitat; and two or more communities/habitats. The biotic and abiotic attributes were determined from the pilot test which identified those attributes cited as being important within a selection of papers across the 11 ecosystem services. It also took into account biodiversity-related indices from other studies (e.g. Feerst, 2006; Feerst et al., 2010; Hooper et al., 2005). The final list of biodiversity attributes included species attributes (presence of a specific species type, species abundance, species richness, species population diversity, species size or weight, population growth rate, mortality rate, natality rate, life span/longevity); functional group attributes (presence of a specific functional group type, abundance of a specific functional group, functional richness, functional diversity, flower-visiting behavioural traits, predator behavioural traits); and community/habitat attributes (presence of a specific community/habitat type, community/habitat area, community/habitat structure, primary productivity, aboveground biomass, belowground biomass, sapwood amount, stem density, wood density, successional stage, habitat/community/stand age, litter/crop residue quality, leaf N content). The final list of abiotic factors included temperature, precipitation, evaporation, wind, snow, soil, geology, water availability, water quality, nutrient availability (soil minerals) and slope (angle, aspect).

The direction of each relationship between the biodiversity attributes of the ESP and the ecosystem service was also classified as being predominantly positive, negative or unclear (i.e. both positive and negative, or authors unsure of the relationship). Where quantitative information on the relationship was provided in the literature, this was also extracted into the database. Furthermore, it was noted whether the paper discussed the ESP as being an ecosystem service antagoniser (ESA[5]), and where biodiversity could also have a negative effect on the ecosystem service concerned. Finally, all papers were evaluated for the strength of the presented findings. This was based on five questions: (i) is the evidence qualitative, quantitative or both?, (ii) is the evidence based on single or multiple observations?, (iii) is the evidence direct or indirect (i.e. through a surrogate)?, (iv) is the link explicitly mentioned or only inferred, and (v) is the evidence based on empirical data, modelled information, or both? Responses to these questions were then combined with equal weighting into a five class qualitative scale ranging from 1 (very weak) to 5 (very strong).

2.2. Data analysis

The collected data were compiled and three variables summarising the linkages between biodiversity attributes and each ecosystem service were calculated: (i) the level of support given – this reflects the number of papers providing the same evidence for a particular linkage; (ii) the strength of evidence – an average ranking of the strength of evidence for the particular linkage ranging from 1 (very weak) to 5 (very strong); and (iii) the direction of the evidence for the relationship – predominantly

[4] ESPs are defined as the component populations, functional groups or communities that contribute to ecosystem service provision (see Harrington et al., 2010 for a more detailed definition).

[5] ESAs are defined as the populations, functional groups or communities which disrupt the provision of other ecosystem services and the functional relationships between them and ESPs (see Harrington et al., 2010 for a more detailed definition).

positive, negative, or unclear (i.e. uncertain). The latter was calculated as follows:

$$\text{Predominant direction} = \frac{\sum\left(\begin{array}{c}\text{Strength of evidence for}\\ \text{all positive relationships}\end{array}\right) - \sum\left(\begin{array}{c}\text{Strength of evidence for}\\ \text{all negative relationships}\end{array}\right)}{\text{Total number of papers showing evidence of relationship}}$$

The parameter “strength of evidence for positive or negative relationships” was chosen rather than raw counts of direction to ensure that those records offering weak evidence had a smaller influence on the overall direction than those identified as having strong evidence. Network diagrams were then created based on the above variables using the Pajek software (http://pajek.imfm.si/doku.php) to explore the linkages between biotic attributes and the individual ecosystem services. Linkages between abiotic attributes and each ecosystem service were also incorporated into the networks based on the number of papers citing a particular linkage.

3. Results

3.1. Linkages between ESPs and ecosystem services

The 11 ecosystem services investigated were found to be underpinned by different ESPs (Table 2), with certain services tending to be linked with certain ESPs. The services freshwater provision, water purification, water flow regulation, mass flow regulation, atmospheric regulation and landscape aesthetics were discussed in at least 70% of papers as being facilitated by a provider at the community level, such as an entire forest, grassland, prairie wetland, high-country landscape or hay meadow. In contrast, the provisioning services of timber production and freshwater fishing were most often facilitated by two or more specific species populations, such as particular species of fish for freshwater fishing or certain tree species for timber production. A particular functional group was often the provider for the regulating services of pollination (in 70% of papers, e.g. flower visiting insects) and pest control (in 30% of papers, e.g. parasitoids). Water flow regulation was the only ecosystem service in this review for which a dominant community was identified as the ESP, although this was mentioned in only two papers.

In general, regulating services were associated with many different ESPs covering the species, functional group and community levels (Table 2). The provisioning services were facilitated by ESPs covering two levels: the species and community levels for freshwater fishing and freshwater provision, and the species and functional group levels for timber production. Not surprisingly, the cultural services were almost exclusively provided at one level: the species level for species-based recreation and the community level for landscape aesthetics.

3.2. Linkages between biodiversity attributes and ecosystem services

A large range of biodiversity attributes (24 out of the 28 listed in Section 2.1) were cited in the papers reviewed as being important for the provision of one or more of the 11 ecosystem services (Fig. 1). The most common were community/habitat area (31% of papers), species abundance, (27%), species richness (25%) and community/habitat structure (24%). Second to these were species size or weight (12% of papers) and community/habitat age (10%). Biomass, including above- and belowground components, and litter were also mentioned in a number of papers, as was species and functional diversity. In contrast, attributes such as wood density, sapwood amount and leaf N content were mentioned in very few papers (less than 2%).

Table 3 provides a breakdown of the important biodiversity attributes by ecosystem service. Timber production and freshwater fishing were most frequently linked to species richness and species abundance, although the latter was also highly related to species size/weight and to a lesser extent to community/habitat area. Pollination was also predominately linked to species richness and abundance, as well as flower-visiting behavioural traits. Species-based recreation was the only other ecosystem service that was mainly linked with species level attributes, with species abundance being the most frequently cited followed by species richness, species size/weight and species diversity.

Freshwater provision, water purification and water flow regulation were most frequently linked with community/habitat area, although community/habitat structure and age were also cited quite often. Landscape aesthetics was also predominantly associated with community level attributes, specifically community/habitat structure and, to a lesser extent, community/habitat area. The services of mass flow regulation, atmospheric regulation and pest regulation show more varied links across different biodiversity attributes. All show the greatest percentage of citations with community level attributes: above- and belowground biomass and community/habitat area and structure for mass flow regulation; community/habitat age and structure and aboveground biomass for atmospheric regulation; and community/habitat structure and area for pest regulation. However, linkages with species level attributes were also found for all three services and with functional group attributes for pest regulation (particularly, functional richness and predator behavioural traits).

Table 2
Percentage of papers citing a linkage between a specific ESP and ecosystem service. The seven ESP classes are: SP1 – single population; SP2+ – two or more populations; FG1 – single functional group; FG2+ – two or more functional groups; DC – dominant community; CH1 – single community/habitat; and CH2+ – two or more communities/habitats. The ESP cited by the greatest percentage of papers are indicated as bold values for each ecosystem service.

Ecosystem service	SP1	SP2+	FG1	FG2+	DC	CH1	CH2+
Provisioning services:							
Timber production	0	**80**	0	20	0	0	0
Freshwater fishing	27	**69**	0	0	0	4	0
Freshwater provision	2	8	0	0	0	42	**48**
Regulating services:							
Water purification	6	10	0	2	0	**54**	28
Water flow regulation (flood protection)	8	20	0	0	4	**50**	18
Mass flow regulation (erosion protection)	4	10	2	10	0	**46**	28
Atmospheric regulation (carbon sequestration)	6	4	2	4	0	**56**	28
Pest regulation (biological control)	20	12	**30**	14	0	20	4
Pollination	6	16	**70**	6	0	0	2
Cultural services:							
Recreation (species-based)	30	**66**	0	0	0	4	0
Landscape aesthetics	0	0	0	0	0	**84**	16

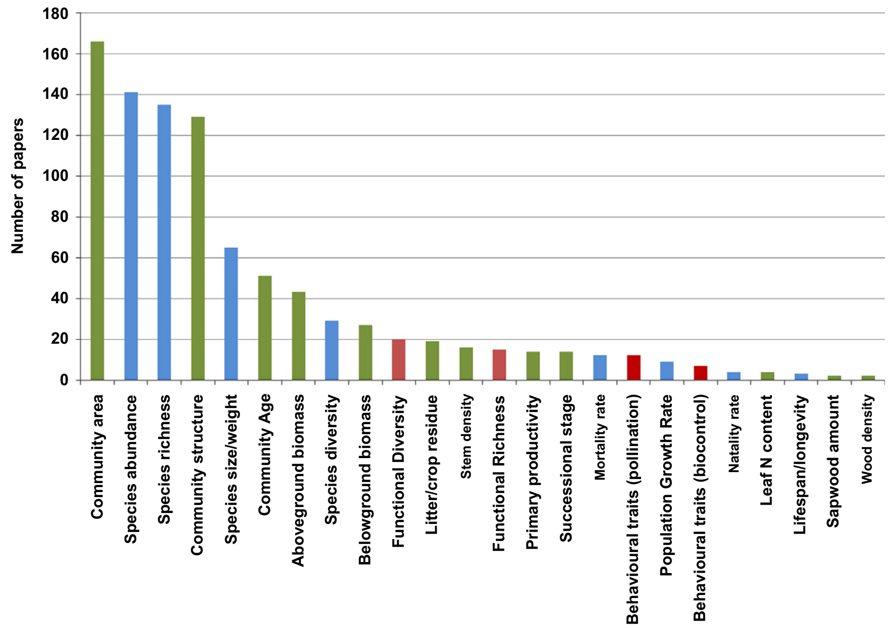

Fig. 1. Number of papers citing a linkage between each biodiversity attribute and the 11 ecosystem services investigated. Bars are coded as: species level attributes – horizontal stripes (blue in web version); functional group level attributes – dots (red in web version); and community or habitat level attributes – diagonal stripes (green in web version).

3.3. Network analysis of linkages between ecosystem services, ESPs, and biotic and abiotic attributes

Specific relationships between ecosystem services, ESPs and their biodiversity attributes have been analysed using network diagrams (see Figs. 2–4 and Online resources). In each network the node in the centre is the ecosystem service, the first tier of nodes linked to the ecosystem service represents the ESP, and the second tier of nodes represents the linkages between the particular ESP and its biotic and abiotic attributes. The width of the connecting lines reflects the number of records showing that linkage, while the colour of the lines reflects the direction of the evidence, i.e. predominantly positive, negative or unclear. Note that information on the direction of relationships was only captured for the biodiversity attributes and not for the ESPs or abiotic factors.

3.3.1. Positive relationships

The majority of relationships between biodiversity attributes and ecosystem services had a dominant positive direction. Figs. 2 and 3 illustrate different patterns of linkages for atmospheric regulation and pest regulation, respectively. For atmospheric regulation (Fig. 2), the majority of papers identify the ESP to be a single or two or more communities. Furthermore, there are positive relationships from these ESPs to many biodiversity attributes, but those with community/habitat structure, age and aboveground biomass are based on the largest number of papers (as also seen in Table 3). For pest regulation (Fig. 3), the pattern of linkages is more distributed with ESPs identified as functional groups, single and multiple species populations and communities/habitats. Most relationships are positive between these ESPs and the biodiversity attributes. Those most cited from all ESPs are community/habitat structure and area, species abundance and richness, functional richness and predator behavioural traits.

Examining the networks for all ecosystem services (see Online resources) shows that species level attributes, such as abundance, were found to benefit species-based recreation, pollination and pest regulation. For example, a higher number of insectivorous birds had a positive effect on pest control (Koh, 2008). Species richness was particularly important for timber production and freshwater fishing, where polycultures were found to be more productive than monocultures (e.g. Erskine et al., 2006 for timber production; and Papoutsoglou et al., 1992 for freshwater fishing). However, it should be noted that although the predominant direction for timber production was positive, eight papers cited a negative relationship with species richness compared to 19 which reported a positive relationship. The size and weight of species is another attribute which positively affected service provision, including freshwater fishing, atmospheric regulation and species-based recreation. In forest environments, it was found that larger trees, such as those with a diameter at breast height (DBH) $\geq$ 10cm account for over 90% of the aboveground carbon stocks in forest and agroforest habitats in eastern Panama (Kirby and Potvin, 2007).

Functional group attributes, such as functional richness and diversity, also displayed a predominantly positive relationship across the services, most commonly discussed for atmospheric regulation, pest regulation and pollination. For the latter two services, the benefits of behavioural traits such as flower visiting behaviour for pollination (Biesmeijer et al., 2006; Hoehn et al., 2008) and natural pest control (Drapela et al., 2011; Lee and McCracken, 2005) were also noted.

Community level attributes, such as community/habitat area, were also found to benefit many ecosystem services, including water purification, water flow regulation, mass flow regulation and landscape aesthetics. Water flow regulation was significantly improved as a result of increased forest area through reducing runoff and providing greater water storage (Farley et al., 2005; Thomas and Nisbet, 2006). A number of papers also discussed a positive relationship with stand age. For atmospheric regulation, larger carbon storage was found in older tree species due to a combination of (a) the time period over which they have sequestered carbon, and (b) the result of tree size increasing with age (e.g. Hantanaka et al., 2011; Keeton et al., 2010; Kirby and Potvin, 2007; Zhao et al., 2010). Numerous papers cited the importance of biomass for carbon sequestration. For example, higher levels of aboveground biomass were linked to increased carbon storage in an alpine meadow (Sun et al., 2011) and a larger green biomass was found to increase soil nitrogen content, in turn increasing soil

Table 3
Percentage of papers citing a linkage between a specific biodiversity attribute and ecosystem service. The biodiversity attributes cited by the greatest percentage of papers are indicated as bold values for each ecosystem service. Note that papers may cite more than one biodiversity attribute linked to an ecosystem service.

Ecosystem service	**Species-level attributes**								**Functional group attributes**			
	Species abundance	Species richness	Species diversity	Species size/ weight	Population growth rate	Mortality rate	Natality rate	Life span/ longevity	Functional richness	Functional diversity	Behavioural traits (pollination)	Behavioural traits (biocontrol)
Provisioning services:												
Timber production	29	**89**	3	3	0	0	0	0	6	9	0	0
Freshwater fishing	**64**	29	2	60	4	11	0	7	0	0	0	0
Freshwater provision	0	2	2	2	4	0	0	0	0	0	0	0
Regulating services:												
Water purification	2	12	4	4	2	0	0	0	2	0	0	0
Water flow regulation	4	0	0	10	0	0	0	0	0	0	0	0
Mass flow regulation	10	14	2	6	0	0	0	0	0	4	0	0
Atmospheric regulation	4	16	16	14	2	12	0	0	0	10	0	0
Pest regulation	40	18	8	6	6	0	4	0	16	6	0	14
Pollination	70	**80**	2	2	0	0	0	0	4	6	22	0
Cultural services:												
Recreation (species)	**72**	34	20	30	0	2	4	0	4	8	2	0
Landscape aesthetics	2	6	0	0	0	0	0	0	0	0	0	0

Ecosystem service	**Community attributes**											
	Community/ habitat area	Community/ habitat structure	Primary production	Aboveground biomass	Belowground biomass	Sapwood amount	Stem density	Wood density	Successional stage	Community/habitat/ stand age	Litter/crop residue quality	Leaf N content
Provisioning services:												
Timber production	0	3	3	3	0	0	9	0	6	0	0	9
Freshwater fishing	22	4	13	13	0	0	0	0	0	2	0	0
Freshwater provision	**56**	12	2	2	6	4	14	0	0	34	0	0
Regulating services:												
Water purification	**62**	16	0	6	2	0	4	0	0	6	2	0
Water flow regulation	**78**	28	0	2	2	0	2	0	4	26	6	0
Mass flow regulation	26	22	0	26	**28**	0	4	0	10	2	8	0
Atmospheric regulation	8	28	6	26	16	0	0	4	6	**30**	12	0
Pest regulation	40	**52**	6	10	0	0	2	0	2	2	10	2
Pollination	4	6	0	0	0	0	0	0	0	0	0	0
Cultural services:												
Recreation (species)	4	2	0	0	0	0	0	0	0	0	0	0
Landscape aesthetics	34	**86**	0	0	0	0	0	0	2	0	0	0

Fig. 2. Network diagram showing the linkages between biotic and abiotic (AF) attributes and atmospheric regulation via various ESPs. The width of the lines reflects the number of papers showing that linkage. The direction of the evidence is indicated by a (+) for predominantly positive relationships (green lines in web version) and a (−) for predominantly negative relationships (red lines in web version) next to the biodiversity attribute. If no direction is indicated the evidence is unclear. The depth of the colour is used to differentiate the strength of the evidence with lighter shades reflecting weaker positive and negative relationships, and darker shades reflecting stronger ones.

carbon, in sub-alpine grasslands (Lavorel and Grigulis, 2012). Landscape diversity (or complexity) was also found to benefit landscape aesthetics. For example, van den Berg et al. (1998) found that beauty ratings were positively related with perceived complexity in The Netherlands, whilst Yao et al. (2012) reported that perceived visual quality was positively influenced by the variety of vegetation in China.

3.3.2. *Negative relationships*

In contrast to the networks for atmospheric regulation (Fig. 2) and pest regulation (Fig. 3), as well as the networks for all other ecosystem services (see Online resources), the network for freshwater provision (Fig. 4) shows predominantly negative relationships between the main ESPs (a single or two or more communities) and different biodiversity attributes. In general it was found that increases in community/habitat area, structure, stem density, aboveground biomass and age increased water consumption and, hence, reduced the provision of this ecosystem service (e.g. Bren and Hopmans, 2007; Farley et al., 2005; Petheram et al., 2002; Zou et al., 2008). For example, increases in afforestation were associated with an average water yield reduction (e.g. Rey Benayas et al., 2007; Sun et al., 2006), as demonstrated by Buytaert et al. (2007) where afforestation of natural grasslands with *Pinus patula* decreased base flow and reduced the water yield by about 50% in a study site on the Andean highlands of Ecuador. Furthermore, in a study of a grassland catchment afforested with *Eucalyptus grandis*, a significant reduction in streamflow was observed with the stream becoming completely dry after a period of 9 years (Scott and Lesch, 1997).

Negative relationships between biodiversity attributes and other ecosystem services are apparent in the networks, but these constitute only a small part of the overall linkages and are generally based on fewer papers than the positive relationships. Such relationships were found with mortality rate and species diversity. For example, atmospheric regulation (Fig. 2) was reduced in grassland communities due to increased mortality of root and rhizome tissues from grazing (Klumpp et al., 2009). Not surprisingly, mortality rate was also found to negatively affect species-based recreation and freshwater fishing by lowering fish stocks (e.g. Lorenzen, 2001). In addition, biodiversity was found to reduce pest regulation in a number of papers (Fig. 3). Reasons cited for this were that (a) in species rich systems, alternative prey can be used as food for predators or parasitoids, decreasing the suppression of pest species (Oelbermann and Scheu, 2009), and (b) that some predators can either become prey themselves (Xu et al., 2011) or protect pests (Mody et al., 2011); both of which decrease the effectiveness of pest control. Note that these negative relationships were mainly found with community/habitat area and structure, but they are not visible in the network for pest regulation (Fig. 3) because a much greater proportion of papers included evidence of positive relationships with the same biodiversity attributes, resulting in a dominant positive direction.

Negative impacts on ecosystem service provision often involved invasive species. For example, rapid growth rates and extensive root systems of species such as *Tamarisk* and *Kandelia candel* were found to increase sedimentation rates, raising surface water elevation and increasing the likelihood of flooding (Foote et

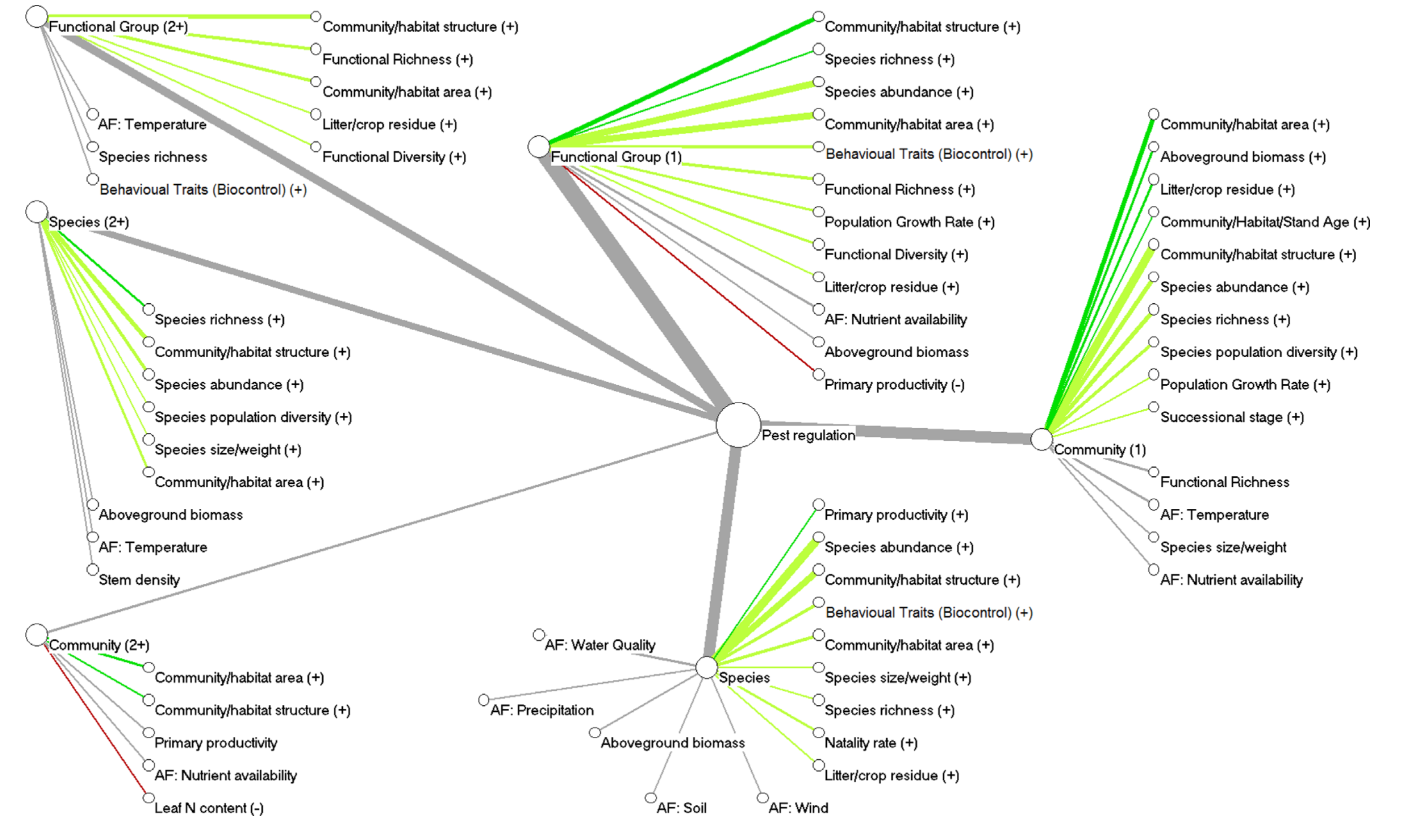

Fig. 3. Network diagram showing the links between biotic and abiotic (AF) attributes and pest regulation via various ESPs. The width of the lines reflects the number of papers showing that linkage. The direction of the evidence is indicated by a (+) for predominantly positive relationships (green lines in web version) and a (−) for predominantly negative relationships (red in web version) next to the biodiversity attribute. If no direction is indicated the evidence is unclear. The depth of the colour is used to differentiate the strength of the evidence with lighter shades reflecting weaker positive and negative relationships, and darker shades reflecting stronger ones.

al., 1996; Lee and Shih, 2004; Zavaleta, 2000). Hence, increases in the area, size and abundance of habitats containing these species negatively affected water flow regulation (Erskine and Webb, 2003). Several studies also reported invasive species antagonising carbon storage and, thus, affecting the service of atmospheric regulation. This was found in forests as a result of bark beetle (*Ips typographus* L.) induced damages (Seidl et al., 2008) and also in Californian grasslands where non-native species, such as *Avena barbata*, were invading native grasses (Koteen et al., 2011). In addition, high densities of the invasive plant dandelion (*Taraxacum officinale*) in the Chilean Andes were found to reduce pollination (Munoz and Cavieres, 2008). Furthermore, the introduction of alien fish species in Mediterranean freshwaters was found to negatively affect native fish populations due to competition for resources and habitat degradation (Hermoso et al., 2011).

3.3.3. Unclear or unknown relationships

The review found that the relationship between biodiversity attributes and ecosystem service provision is not always simple (i.e. predominantly positive or negative). Hence, there were instances where the relationship between certain attributes and a given ecosystem service was classified as unclear. This could occur due to the existence of a threshold after which the direction of the relationship with the biodiversity attribute changed, such as was reported in 34% of papers for the effect of species abundance on freshwater fishing. Often a higher abundance of fish species increased the provision of this service, however, once a certain level or ecological carrying capacity was breached, fish yield was found to decrease (e.g. De Silva et al., 1992; Hasan and Middendorp, 1998; Lorenzen, 1995; Smith et al., 2012). A similar effect was observed in a study of mass flow regulation by Cammeraat et al. (2005) in which root systems of early successional vegetation on steep slopes were associated with increased erosion, but this effect was reversed after a period of 40 years when later successional plant communities with different root systems had established.

Unclear relationships may also result from conflicting evidence both within and between papers. This was found for two papers considering linkages between species diversity and atmospheric regulation (e.g. Potvin et al., 2011; Sharma et al., 2010) as is apparent from the network shown in Fig. 2, where this biodiversity attribute has a positive relationship with a single community ESP and a negative relationship when two or more communities were identified as the ESP. Interactions between species can also lead to unclear relationships. For example, bees, particularly managed honey bees, can have indirect negative effects on pollination services by competing with wild pollinator species for flower resources and reducing flower visitations by the latter (Allsopp et al., 2008; Shavit et al., 2009). This led to 14% and 10% of relationships for pollination with species abundance and species richness, respectively, being defined as unclear. The effect of community/habitat structure on pest regulation was also unclear in 18% of papers. For example, Bianchi et al. (2010) found that dispersal and gathering behaviour of predator groups influenced their performance, although this was in turn influenced by landscape structure.

3.3.4. Abiotic factors

The influence of abiotic factors, in addition to biotic attributes, on ecosystem service provision was also considered in our review

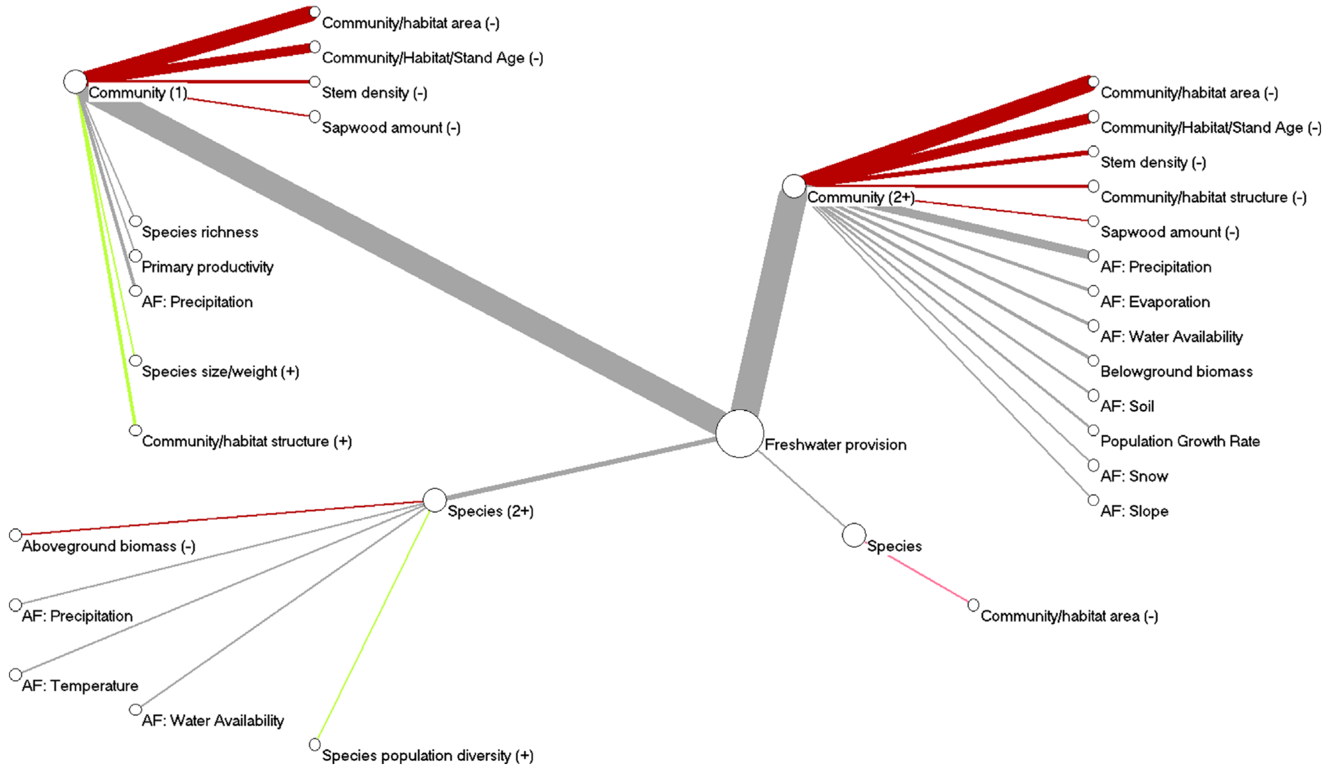

Fig. 4. Network diagram showing the linkages between biotic and abiotic (AF) attributes and freshwater provision via various ESPs. The direction of the evidence is indicated by a (+) for predominantly positive relationships (green lines in web version) and a (−) for predominantly negative relationships (red lines in web version) next to the biodiversity attributes. If no direction is indicated the evidence is unclear. The depth of the colour is used to differentiate the strength of the evidence with lighter shades reflecting weaker positive and negative relationships, and darker shades reflecting stronger ones.

and integrated into the network diagrams (Figs. 2–4). Although the search strategy was directed towards literature focusing on biotic attributes affecting the ecosystem services, 22% of papers specifically mentioned a link between an abiotic factor and service delivery. They are an integral part of the ESP (Harrington et al., 2010) and it is hardly surprising that climatic parameters such as temperature and precipitation were commonly cited, particularly for the services of atmospheric regulation, mass flow regulation, water flow regulation, water purification and freshwater provision, where these abiotic parameters often have direct, clearly observable influences. Further abiotic factors that were identified in greater than 10% of papers for at least one ecosystem service were soil properties such as porosity (cited across many services), water quality and nutrient availability (particularly cited for freshwater fishing), and slope (particularly cited for mass flow regulation).

4. Discussion and conclusions

Previous studies have provided valuable information on the role of biodiversity in ecosystem service delivery from a theoretical perspective (Mace et al., 2012), explored the links between functional traits and ecosystem services (de Bello et al., 2010) or examined how biodiversity influences the functioning of ecosystems and, thus, their ability to provide ecosystem services (Cardinale et al., 2012). In this study we have gone a step further to build up the scientific knowledge base on ESPs, their biodiversity attributes, the direction and strength of evidence for these relationships, the influence of abiotic factors, and the visualisation of the linkages using network analysis. The results show an intricate array of linkages between biodiversity attributes related to ESPs and ecosystem services. Overall, our results add weight to the emerging realisation that the relationships between biodiversity and the provision of ecosystem services are highly complex and involve many uncertainties (Balvanera et al., 2014).

The detailed networks for each of the selected ecosystem services demonstrate particular hierarchies and the immense complexities of the relationships between biodiversity and service provision. Nevertheless, some dominant trends emerge. Five biodiversity attributes stand out as being particularly important with each being cited in over 50% of papers for at least one ecosystem service. These are species abundance (freshwater fishing, pollination, species-based recreation), species richness (timber production, pollination), species size/weight (freshwater fishing), community/habitat area (freshwater provision, water purification, water flow regulation) and community/habitat structure (pest regulation, landscape aesthetics). Three further biodiversity attributes are notable, being reported in between 25 and 50% of papers for at least one ecosystem service: community/habitat age (freshwater provision, atmospheric regulation, water flow regulation), and above- and belowground biomass (mass flow regulation and atmospheric regulation). These dominant attributes tend to be at the species and community levels, but functional group attributes were also frequently cited as being important for pollination and pest regulation (in 14 to 22% of papers). Some of these relationships may appear to be commonplace or a matter of trivial logic, but we believe that this is the first time that such linkages have been clearly documented in a comparative context.

Although it may be tempting to consider only the “simpler” pattern of thicker lines, representing the most often cited links in the network diagrams, it is the inclusion of the less frequently cited linkages of thinner lines, which may be functionally just as important, that reveals the full degree of interdependence and complexity across organisational levels. A summary of the linkages between broad categories of biodiversity attributes, ESPs and ecosystem services for all the services included in this review is provided in Fig. 5. This emphasises the range of organisational levels involved in the overall relationship between biodiversity and ecosystem services with each service being linked to a number of ESPs and biodiversity attributes that together span multiple spatial scales. The attributes identified at a particular organisational level can be of importance to ESPs operating at different levels of organisation. For example, an attribute of a species population such as "abundance of individuals" can have important links to ESPs that are defined at the functional group level (e.g. pollinators) or at entire community levels (e.g. atmospheric regulation). Similarly, functional group or community level attributes (e.g. functional richness, community/habitat area) can be important for ESPs that work on one or more species' population levels. Note that it is equally valid to view these links from the opposite direction, so that it may be said that ESPs operating at any particular scale draw upon biodiversity attributes that are characteristic of a variety of different organisational levels. The important point is that there is an interdependence between ESPs and their attributes that feeds the delivery of the different ecosystem services via a very complex network that is a consequence of the range and variety of linkages within the detailed networks associated with the single services (Figs. 2–4). This is supported by the literature review of de Bello et al. (2010) who provides a similar diagram to Fig. 5 highlighting the multiple associations between traits and ecosystem services across different organisational levels.

In addition to identifying the linkages between biodiversity attributes and ecosystem services, the direction of the relationship (positive, negative or unclear) was captured wherever possible (as summarised in Table 4 for relationships cited in at least 10% of papers). This confirms the strong evidence base supporting a positive relationship between community/habitat area and water purification and water flow regulation, between community/habitat structure and landscape aesthetics, and between species richness and pollination. It also shows that considerable uncertainties still exist for some relationships with evidence being spread across different attributes, or evidence being mixed (i.e. showing both positive and negative trends). This is supported by Cardinale et al. (2012) who also found that evidence for effects of biodiversity on ecosystem services was often mixed. In their review of relationships between different diversity levels (species, genetic and trait) and a range of provisioning and regulating ecosystem services, positive trends were found for wood, fisheries, carbon storage, pollination and freshwater purification and negative trends for pest control. The results are not directly comparable with our study, but together they considerably increase the evidence base and highlight gaps in knowledge.

Although attention is usually focussed on the positive linkages, and these dominate in the present literature review (Table 4), the negative relations between biodiversity and ecosystem service provision are also very important to the overall dynamics. The components of biodiversity responsible, the ESAs, can be defined at any level and may have direct or indirect disruptive effects on service provision (Harrington et al., 2010). Importantly, what is a provider for one service (i.e. an ESP) can at the same time act as an ESA for other services. For example, many links between biodiversity attributes and the provision of freshwater were predominantly negative (Fig. 4) because vegetation parameters such as increased stem density, biomass and age, particularly in relation to trees, have a direct negative effect by sucking water out of the system. However, these same vegetation attributes may be important for the provision of many other services not considered in these studies, such as atmospheric regulation or landscape aesthetics.

We also found that regulating services were often associated with more ESPs and biodiversity attributes than other categories of ecosystem services as shown in Tables 2 and 3 (based on the 11 services investigated in this study). This is supported by analysis of the network diagrams which shows that the linkages were generally more complex and branched (i.e. each node was associated with a greater number of connections) for regulating services (as shown in Figs. 2 and 3 for

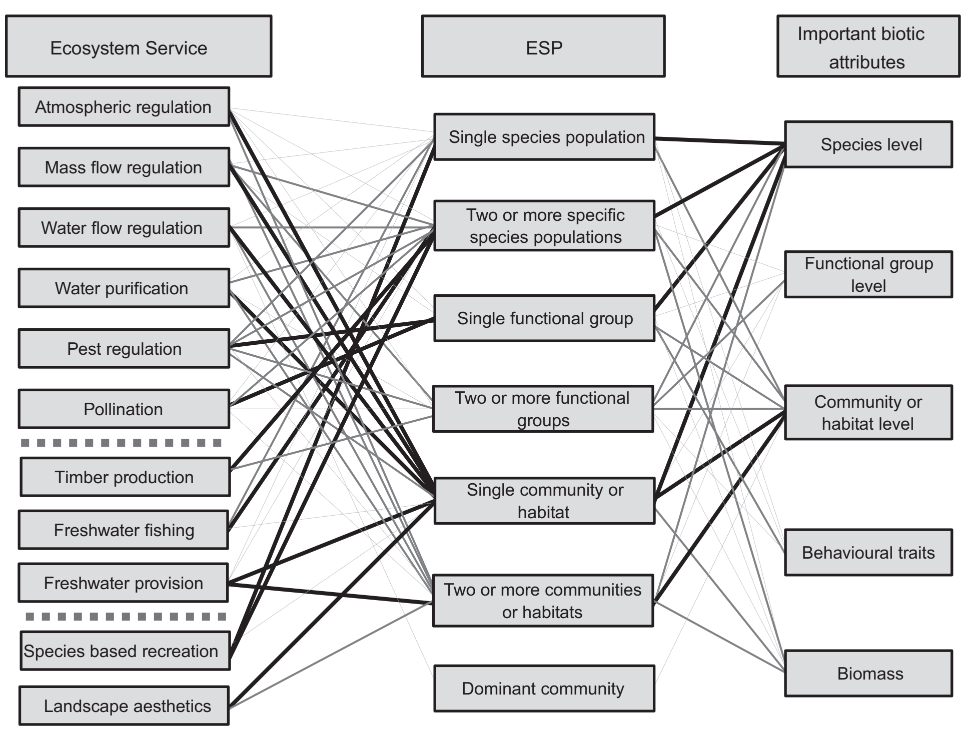

Fig. 5. Linkages between broad groups of biodiversity attributes, ESPs and ecosystem services for the 11 ecosystem services included in the literature review. Species level attributes include species richness, diversity, abundance, size and weight; functional group level attributes include functional diversity and functional richness; community or habitat level attributes include community/habitat area, age, structure and successional stage; behavioural traits include flower visiting behaviour and biocontrol; and biomass attributes include above and belowground biomass and litter or crop residue. The thickness of the connecting lines reflects the number of papers providing evidence for that linkage equally divided into three categories with the thickest lines representing the most frequently cited linkages.

Table 4
Summary of positive and negative relationships between biodiversity attributes and ecosystem services. Note only relationships found in greater than 10% of papers are included. Arrow direction indicates positive (↑) or negative (↓) relationship. Arrows in bold based on ≥50% of papers; arrows not in bold based on 10–49% of papers.

	Species abundance	Species richness	Species diversity	Species size/weight	Mortality rate	Functional richness	Behavioural traits (pollination)	Behavioural traits (biocontrol)	Community/habitat area	Community/habitat structure	Primary production	Aboveground biomass	Belowground biomass	Stem density	Community/habitat/stand age	Litter/crop residue quality
Provisioning services:																
Timber production	↑	**↑**↓														
Freshwater fishing	↑	↑		↑	↓						↑					
Freshwater provision									↑↓					↓	↓	
Regulating services:																
Water purification		↑							**↑**							
Water flow regulation									**↑**	↑					↑	
Mass flow regulation		↑							↑	↑		↑	↑			
Atmospheric regulation		↑	↑	↑	↓					↑		↑	↑		↑	↑
Pest regulation	↑	↑				↑		↑	↑	↑						↑
Pollination	↑↓	**↑**					↑									
Cultural services:																
Recreation (species)	↑↓	↑	↑	↑												
Landscape aesthetics									↑	**↑**						

atmospheric regulation and pest regulation) compared to provisioning services (as shown in Fig. 4 for freshwater provision). This stresses the significant role that biodiversity plays as a regulator of ecosystem processes (Mace et al., 2012). It also highlights the importance of further research to understand how different services interact with each other and the biodiversity attributes that underpin them, as the condition of regulating services (often referred to as intermediate services by some authors; e.g. Fisher et al., 2009) can be critical in mediating the delivery of other services.

Our review focused on a sample of ecosystem services across the different service categories and did not consider interrelationships between services. Information on such aspects could be extracted from the papers which emerged from this review, but a different approach specifically focused on assessing synergies and trade-offs between ecosystem services and their relationship to the underlying biodiversity may reveal new insights. Further research to expand the search to cover more services and to explore how the linkages identified differ by ecosystems or biogeographical region would also be useful for targeting the management of biodiversity and service provision. The complex relationships we have reported here are based on only the frequencies of citation in the literature, which is not necessarily the same as functional importance. Nevertheless, the results could be used to guide which biodiversity attributes should be the focus of future research to advance understanding of the functional importance of biodiversity for ecosystem service supply. More specifically, additional research is needed to better understand the linkages represented by the thin lines in the networks – the linkages exist, but how strong are their functional roles in joining the different aspects of biodiversity with the provision of ecosystem services in the amounts required by beneficiaries?

Our review focuses on the links between the biophysical elements of biodiversity and ecosystem services. However, to support management and protection strategies, future research should also take account of effects of socio-economic factors and land use decisions on different components of biodiversity and, as a result, ecosystem service delivery. Incorporating traditional conservation strategies for species and habitat protection within the broader context of social-ecological systems and ecosystem service delivery can lead to added benefits for biodiversity through closer integration of conservation policy with policies in other sectors (Haslett et al., 2010). This approach usefully extends conservation effort beyond the borders of protected areas, to encompass many species with presently widespread distributions as well as other aspects of biodiversity occurring in non-protected areas. But the social-ecological system approach also has the capacity to considerably improve conservation management effectiveness within protected areas (Palomo et al., 2014). Biodiversity is not (just) a good to be conserved for its intrinsic value, but has a critical role in ecosystem processes (Mace et al., 2012) that provide essential services to humans (Cardinale et al., 2012). Improving understanding of when the goals of biodiversity conservation and ecosystem service maintenance are compatible or interdependent (Balvanera et al., 2014) requires a strong knowledge base on biodiversity–ecosystem service linkages within different socio-ecological systems. Further expansion of this knowledge base through closer examination of the less well studied relationships depicted in this review may help to reveal additional or new arguments for the need to conserve biodiversity in all its guises.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.ecoser.2014.05.006.

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