How natural capital delivers ecosystem services: a typology derived from a systematic review

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Abstract

There is no unified evidence base to help decision-makers understand how the multiple components of natural capital interact to deliver ecosystem services. We systematically reviewed 780 papers, recording how natural capital attributes (29 biotic attributes and 11 abiotic factors) affect the delivery of 13 ecosystem services. We develop a simple typology based on the observation that five main attribute groups influence the capacity of natural capital to provide ecosystem services, related to: A) the physical amount of vegetation cover; B) presence of suitable habitat to support species or functional groups that provide a service; C) characteristics of particular species or functional groups; D) physical and biological diversity; and E) abiotic factors that interact with the biotic factors in groups A-D. 'Bundles' of services can be identified that are governed by different attribute groups. Management aimed at maximising only one service often has negative impacts on other services and on biological and physical diversity. Sustainable ecosystem management should aim to maintain healthy, diverse and resilient ecosystems that can deliver a wide range of ecosystem services in the long term. This can maximise the synergies and minimise the trade-offs between ecosystem services and is also compatible with the aim of conserving biodiversity.

Keywords

Biodiversity; functional diversity; trait; attribute; trade-offs; land management.

1 Introduction

Natural capital is the elements of nature that directly or indirectly produce value for people, including ecosystems, species, freshwater, land, minerals, air and oceans, as well as natural processes and functions (Mace et al., 2015; Potschin et al., 2016). It thus comprises both biotic components (living organisms and non-living biotic matter such as leaf litter) and abiotic components (rocks, minerals, air, water). These components interact to deliver the ecosystem services that are vital to human wellbeing, sometimes with additional input from social, human, financial or manufactured capital assets (Biggs et al. 2015; Palomo et al. 2016; Reyers et al. 2013).

It is more than ten years since the Millennium Ecosystem Assessment revealed that 60% of ecosystem services were at risk due to unsustainable use (MA, 2005), yet the stocks of natural capital from which these services flow are still shrinking due to habitat degradation and species loss (Costanza et al., 2014). Decision-makers in policy, practice and business are increasingly aware of the need to manage natural capital sustainably, but they lack suitable tools and evidence to enable them to assess the impact of different management decisions (Guerry et al., 2015; Maseyk et al., 2017). In particular, there is a lack of understanding on how the biotic and abiotic attributes of natural capital influence the capacity of ecosystems to supply different services (Maseyk et al., 2017).

There is also considerable debate over the compatibility of the ecosystem services approach with the goals of biodiversity conservation. The ecosystem services approach offers opportunities to develop broader constituencies for conservation and to expand possibilities to influence decision-making (Haslett et al., 2010; Ingram et al., 2012; Reyers et al., 2012), as well as adding new value to protected areas (García Llorente et al., 2016), and promoting sustainable management of ecosystems outside of protected areas (Haslett et al., 2010). Various studies have demonstrated a certain degree of spatial congruence between areas that have high biodiversity and those that have high potential to deliver ecosystem services (e.g. Egoh et al., 2009; Maes et al., 2012; Strassburg et al., 2010) or shown that land use scenarios that favour biodiversity conservation can also benefit ecosystem service provision (e.g. Nelson et al., 2009). However, there is growing concern that focussing on the provision of benefits for humans may conflict with conservation priorities (Schröter et al., 2014) and that win-wins for people and wildlife are hard to achieve in practice (McShane et al., 2011). A focus on single ecosystem services may result in additional exploitation of ecosystems, e.g. for provision of food or timber; rare or endemic species that are of high conservation interest may have no obvious value for ecosystem service provision; and it may seem that ecosystem services can be delivered adequately by areas with very limited biodiversity value (Ingram et al., 2012).

In order to design management strategies that can deliver the multiple ecosystem services required to sustain quality of life for people at the same time as maintaining healthy and diverse ecosystems with space for wildlife, in line with the Sustainable Development Goals, we need to understand:

i. what natural capital attributes are important for delivering different services, including both biotic attributes and abiotic factors;
ii. what are the potential synergies or trade-offs between different bundles of services;
iii. what management strategies can deliver benefits for multiple ecosystem services and minimise conflicts between different priorities?

This knowledge is critical to inform the sustainable long-term management of natural resources, to manage trade-offs and synergies between different services, and to design ecosystem management strategies that are compatible with the goals of biodiversity conservation (Mace et al., 2012).

There is evidence on the links between natural capital attributes and ecosystem services in the scientific literature, but it is highly fragmented. A systematic review by Harrison et al. (2014) that searched for links between 11 ecosystem services and 28 biotic natural capital attributes found 530 individual studies, but most of these focus on just one service and only a few natural capital attributes, most commonly habitat area, species abundance or species richness. Similar reviews have made useful advances but they often focus mainly on the natural capital attributes that are related to biological diversity, such as species richness or functional diversity, neglecting other attributes such as species abundance or habitat area (e.g. Balvanera et al., 2014; Cardinale et al., 2012; Cimon-Morin et al., 2013; Lefcheck et al., 2015); or cover a smaller range of ecosystem services (Balvanera et al., 2014; Ricketts et al., 2016); or focus on a particular case study context (Bastian, 2013) or ecosystem type (Isbell et al., 2011).

The review by Harrison et al. (2014) increased our understanding of how ecosystem service delivery is governed by a variety of biotic attributes such as the area of specific habitats, the abundance of particular species and the diversity of functional traits. However, it also identified the need to extend coverage to include further ecosystem services, to fill in knowledge gaps, to address interactions between services (synergies and trade-offs), and to gather information on the influence of ecosystem condition, especially on the existence of any thresholds beyond which service delivery could be compromised. In addition, although Harrison et al. (2014) demonstrated the complexity of the patterns of links between multiple natural capital attributes and ecosystem services, there is still a need for a simpler framework to enable the knowledge synthesised by the review to be applied in practice by land use managers and other decision-makers.

This study therefore builds on the work of Harrison et al. (2014), updating and extending it significantly to cover 13 ecosystem services, including new research carried out since the review date of 2012, and recording new evidence on: (i) the influence (positive, negative or mixed) of both biotic attributes and abiotic factors on service delivery; (ii) the effect of ecosystem condition on service delivery; (iii) the presence of any thresholds; (iv) the impact of human management and policies on ecosystem service delivery; and (v) qualitative or quantitative information on synergies or trade-offs between services.

This study aimed to:

- build a coherent database that identifies the structural and functional factors (natural capital attributes) that link natural capital stocks to ecosystem service flows in different contexts, thus increasing understanding of the biophysical control of ecosystem services;
- evaluate the feasibility of detecting possible thresholds where further biodiversity loss would severely compromise ecosystem functioning and service delivery;
- develop a simple typology for understanding and classifying the links between natural capital and ecosystem service delivery, to help reduce complexity and to guide the application of the ecosystem service approach in research, policy and practice for sustainable land, water and urban management;
- apply the results of the review to explore whether the ecosystem services approach is compatible with conservation objectives, especially regarding the impact of biological diversity on service delivery.

2 Method

The review covers a representative selection of the most commonly studied ecosystem services: four provisioning services (freshwater fishing; timber production; food crop production; water supply), seven regulating services (air quality regulation; atmospheric regulation via carbon sequestration; mass flow regulation via erosion protection; water quality regulation; water flow regulation via flood protection; pollination; pest regulation) and two cultural services (species-based recreation and aesthetic landscapes).

The search conformed to the methodology developed during the BESAFE project (Harrison et al., 2014). The search protocol used a standard set of terms to cover the biotic attributes of interest (e.g. “richness”, “trait”, “habitat”), plus a set of keywords specific to each ecosystem service (e.g. “carbon storage”). This strategy usually returned thousands of articles, many of which were not relevant – for example, many dealt with the impact of activities such as fishing or crop production on natural capital, rather than the other way round. Additional service-specific terms were therefore used if necessary to refine results. The full list of search terms is presented in Appendix A of the Supplementary Material.

The search was carried out using Web of Science and covering articles published up until the end of June 2014. Web of Science was chosen because it provides full coverage of the relevant journals across many different disciplines, and because it is possible to enter complex search strings.

Because of the large number of results returned, the analysis for each service was restricted to the first 60 articles that met the study criteria when the search results were ordered in terms of relevance according to the keyword search string used in the Web of Science search engine, making a total of 780 articles. For services where the hit rate for relevant articles was low, the search was supplemented by snowballing (examining the reference lists of the most relevant articles) and reverse snowballing (looking for articles that cite the most relevant articles).

Each article reviewed was analysed in detail and the following information was recorded in a database:

- the ecosystem service covered;

- the location of the study (geographical co-ordinates and place name);
- type and condition of ecosystems, including whether they are actively managed;
- the main ecosystem service provider (ESP): this can be an entire community or habitat (such as a forest or lake); a functional group (such as pollinating insects); or one or more individual species;
- the biotic attributes that affect service delivery, and their direction of influence (positive, negative, both or unclear) (see Appendix B of the Supplementary Material for a full list);
- the abiotic factors which affect service delivery, and their direction of influence see Appendix B of the Supplementary Material for a full list);
- the indicators used to assess the level of service provision (see Appendix C of the Supplementary Material)
- any qualitative or quantitative information on interactions between different ecosystem services, and the direction of interaction;
- any qualitative or quantitative information on human input and management, and its direction of impact;
- any evidence for thresholds or tipping points.

We also recorded other information including the spatial and temporal scale of the study and the type of evidence presented in the paper. However these are not discussed in this paper, which focuses on the biotic and abiotic attributes, the interactions between ecosystem services and the impact of any human input or management.

The 13 ecosystem services were allocated across a team of 16 reviewers according to their expertise. This large number introduced the potential for inconsistency between different reviewers, so a final quality check of the database entries across all services was undertaken by a single reviewer.

In order to gain a full understanding of the factors linking natural capital attributes to ecosystem service delivery, the scope of the review was very wide, covering 29 biotic attributes, 11 abiotic factors and 13 ecosystem services. The studies reviewed included a wide range of experimental and observational approaches and used many different indicators (see Appendix C in the Supplementary Material). It was therefore necessary to use a vote-counting approach, because meta-analysis was not possible for such a diverse dataset using so many incompatible indicators and approaches.

The database was analysed by generating descriptive statistics based on the frequency of citations related to different biotic attributes and abiotic factors, and their direction of influence. This analysis was performed across all services and also individually for each service. Network diagrams were created for each ecosystem service to illustrate the links with abiotic factors and biotic attributes. In these diagrams, generated with the Pajek software, the thickness of the lines is proportional to $n^{0.1}$ where n is the number of papers supporting the existence of a link (including unclear links). The colour of the lines refers to the predominant direction of the links, with dark red or green indicating where all papers support a negative or positive link respectively, and light red or green indicating where the link is “mostly negative” or “mostly positive”, i.e. at least one paper supports the opposite direction. Grey indicates either that all links are unclear, or that there are equal positive and negative links (‘neutral’). In these diagrams we group the attributes into the following categories.

- Habitat: community or habitat characteristics such as type, area, successional stage, biomass and stem density. Community structure is included under ‘diversity’ (see below).

- Species or functional group: characteristics such as type, abundance and species size or behaviour.
- Diversity: biological (species richness, functional diversity etc.) and physical (landscape diversity and community/habitat structure, which generally refers to structural diversity).
- Population dynamics: mortality rate, natality rate, life span and population growth rate. These attributes can be related to particular species but are also partly influenced by environmental conditions and human activity. They may affect many of the attributes in the other categories.
- Other (attributes appearing in the literature but not pre-defined in the review database).

These categories form the primary nodes in the network diagrams, and the individual attributes form the secondary nodes. Similar diagrams were also created to summarise the pattern of evidence for positive and negative interactions between different ecosystem services.

In all these network diagrams, the line thickness indicates only the number of papers citing the existence of a link: this is not necessarily equivalent to the strength or importance of the link. The absence of a link, or a thin line, does not necessarily mean that no link exists, but that there is currently no evidence or only weak evidence for such a link in the literature base.

Visual examination of the network diagrams and the tabulated results of the review enabled the researchers to develop a simple typology for classifying the ways in which natural capital supports ecosystem services.

3 Results

3.1 Links between natural capital attributes and ecosystem services

The literature reviewed is dominated by evidence on the positive influence of natural capital attributes on ecosystem services (Table 1a) with few examples of negative influence (Table 1b). Of the 2607 links identified in the 780 studies, 73% are positive, 9% are negative, 7% show both positive and negative impacts, and for 11% the direction of influence is unclear. The red lines in Table 1b highlight the two most commonly cited negative influences, in the column for mortality rate — often as a result of human activity that leads to degradation of ecosystems — and the row for water supply, where timber plantations can reduce supply in water-scarce regions (see section 3.1.4).

Community/habitat area is the attribute that is most often found to influence service provision, in 37% of studies (Figure S1, Supplementary Material). This reflects the large number of studies that focus mainly on the size of the area covered by an ecosystem, such as studies on the relationship between forest area and flood risk. Of the other habitat-related attributes, habitat type and structure are each cited in 31% of studies. A link to the presence of a specific species is found in 34% of studies, and a link to species abundance in 17% of studies. The most commonly cited species-specific attribute is size/weight (in 13% of studies). The presence and abundance of specific functional groups (such as ‘trees’ or ‘pollinators’) is found to be significant in 21% and 11% of studies respectively. Of the diversity-related attributes, a link to species richness is found in 30% of studies. Functional diversity and functional richness are investigated less often, but are found to be important in 9% and 6% of studies, respectively. Some attributes, including sapwood amount (0.5%), wood density (1%) and natality rate (1.3%), are mentioned very rarely.

The literature search focused on biotic attributes, but we also recorded the impact of any abiotic factors that are mentioned in the articles. Abiotic factors can affect service delivery directly (e.g. through the role of precipitation in improving water supply) or indirectly, by affecting the condition of the ecosystem. A range of factors are found to influence service provision, with precipitation, soil type and temperature being the most frequently cited, but the direction of impact is variable and highly dependent on the context (Figure S2, Supplementary Material). For example, heavy precipitation may reduce the ability of ecosystems to provide flood protection if the ground becomes saturated, but lack of precipitation may lead to forest dieback which will reduce provision of flood protection and many other services. Note that soil type, geology and 'other' are categorical rather than quantitative variables so it was not meaningful to record the direction of impact, and these impacts are therefore all recorded as 'unclear'.

The breakdown of positive and negative links for each ecosystem service (see Table 1 for biotic factors; Tables S1 and S2 for abiotic factors) reveals some interesting patterns. Bundles of ecosystem services can be identified, which are influenced by different broad groups of natural capital attributes (Figure 1). In this section we present an overview of the main findings, which leads to the development of a simple typology for classifying the links. This is underpinned by more detailed descriptions and network diagrams for each service, which are presented in the Supplementary Material (Figures S3 to S15). Further details are available in a technical report (Perez-Soba et al., 2017).

Figure 1: Network diagram mapping the evidence on how groups of biotic attributes and abiotic factors influence bundles of ecosystem services. Line thickness is proportional to number of studies supporting each link and line colour indicates predominant direction of link. For abiotic factors the links are all shown as neutral because the direction of influence is highly context-dependent. When interpreting line thickness, note that the bundles contain different numbers of services (the air, water and soil bundle contains five services; pollination and pest regulation and food and timber provision contain two services; the rest contain only one service).

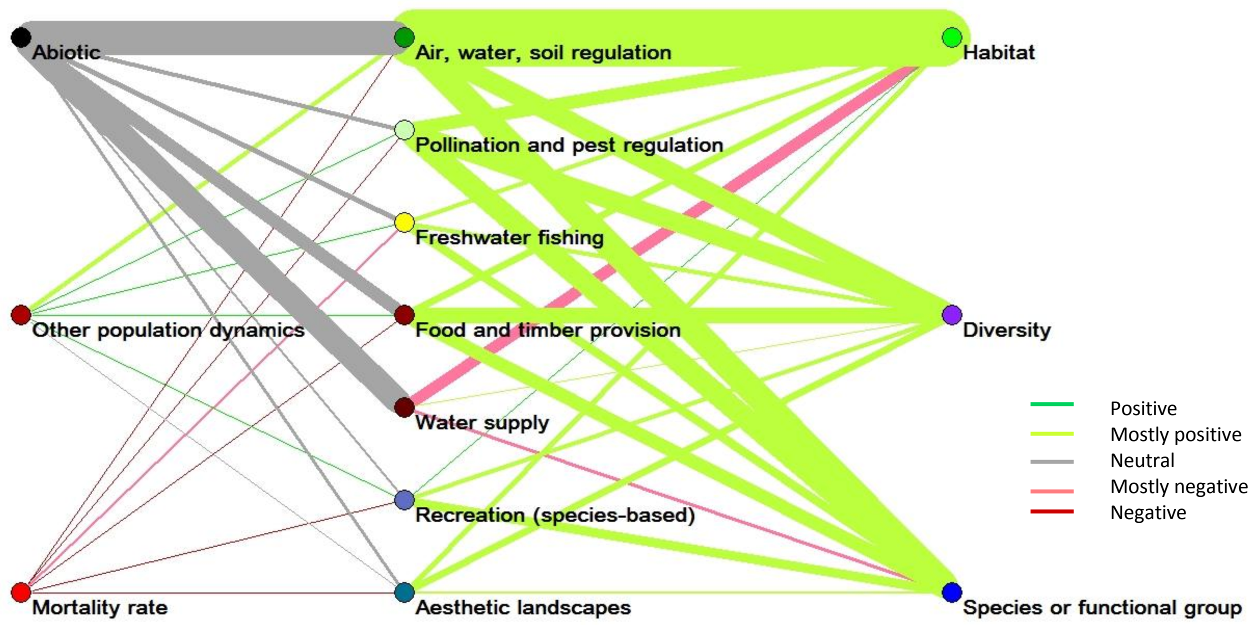


Table 1a: Number of studies showing a positive link (not including mixed or unclear) between an ecosystem service and a specific biotic attribute. More frequently cited links are highlighted in darker shades of green. Total number of studies reviewed for each service = 60.

	Community / habitat										Diversity					Specific species or functional group										Population dynamic				
	Presence of a specific community/habitat	Community/habitat area	Community/habitat structure	Community/habitat/stand age	Successional stage	Primary productivity	Aboveground biomass	Belowground biomass	Stem density	Litter/crop residue quality	Landscape diversity	Species richness	Functional richness	Functional diversity	Species population diversity	Presence of a specific functional group	Abundance of a specific functional group	Presence of a specific species type	Species abundance	Species size/weight	Wood density	Sapwood amount	Leaf N content	Flower-visiting behavioural traits	Predator behavioural traits (biocontrol)	Population growth rate	Life span/longevity	Natality rate	Mortality rate	Other biotic
Air quality regulation	5	27	4	1		2	5		1			4	1	1	1	12	3	15	2	9							1			18
Atmospheric regulation	12	17	14	18	8	9	35	25	2	6		16	2	8	5	6	8	15	4	12	6		1			8	2			1
Water flow regulation	5	41	21	10	2		1	2		2						4	3	3	1	3						1				1
Mass flow regulation	34	31	28	5	8	1	11	21	8	14		7	3	7		22		20	1	3						7				1
Water quality regulation	40	37	8	3	1	3	5	5	4	3		6	1	3	2	7	4	17	6	6						1				
Pollination	22	15	19						1		8	25	10	11	7	32	21	17	20	3				15						4
Pest regulation	17	20	22	1	2	1	2		1	5	5	9	8	7	1	10	13	4	11	1					11	3	2	2		5
Freshwater fishing	12	12	10		1	6	1			2	5	8	1	1	4	4	2	16	17	21			1			6	1	2	1	
Timber production	1		7	2	1	1	2		7	3		35	5	9		6		18	7	4		1	6			2				
Food production (crops)	1	4	2				11	8		10	1	35	4	5	11	23	9	19		1			10			7				
Water supply	8	7	5	2	1			2	1	1		1			1	2		1		1										1
Recreation (species-based)	4	3										18	1	3	10	7	5	43	15	10								2		6
Aesthetic landscapes	26	7	34	2	1		1		2		7	8		2		1		5	2	3										3

Table 1b: Number of studies showing a negative link (not including mixed or unclear) between an ecosystem service and a specific biotic attribute. More frequently cited links are highlighted in darker shades of red. Total number of studies reviewed for each service = 60. Red lines highlight that most of the negative impacts are related to mortality rate and water supply.

	Community / habitat										Diversity					Specific species or functional group										Population dynamic				
	Presence of a specific community/habitat	Community/habitat area	Community/habitat structure	Community/habitat/stand age	Successional stage	Primary productivity	Aboveground biomass	Belowground biomass	Stem density	Litter/crop residue quality	Landscape diversity	Species richness	Functional richness	Functional diversity	Species population diversity	Presence of a specific functional group	Abundance of a specific functional group	Presence of a specific species type	Species abundance	Species size/weight	Wood density	Sapwood amount	Leaf N content	Flower-visiting behavioural traits	Predator behavioural traits (biocontrol)	Population growth rate	Life span/longevity	Natality rate	Mortality rate	Other biotic
Air quality regulation							1									1													2	3
Atmospheric regulation			1				2					1		1				2									1		8	1
Water flow regulation	1	3		1					1							1		1	3	1										
Mass flow regulation	1		1	1	2											2		2		2										
Water quality regulation				2	1					1							1	1		2			1							
Pollination		1																2	2											
Pest regulation			2				1																1						2	1
Freshwater fishing												1						1		1									14	
Timber production			1		3				4			5	1	2		3	1												2	
Food production (crops)								1				1				1		2											1	
Water supply	20	26		12			2	2	9	1						5	1	10		2		2				5				1
Recreation (species-based)												2			1				5										5	
Aesthetic landscapes			1															1	1										1	

3.1.1 Air, soil and water regulation

There is a bundle of five services related to air, soil and water regulation (Figures S3 to S7). For three of these services — atmospheric regulation (carbon storage), water flow regulation (flood protection) and water quality regulation — the literature is dominated by studies focusing on entire habitats. Often two or more habitats are compared, e.g. forest and grassland, or natural forest and plantation. Typically the studies find that the service is related to the amount of vegetation cover and the quantity of biomass per unit area, so forests tend to offer a higher level of service than shrubland or grassland, and the service increases in forests with older and larger trees. For example, larger trees store more carbon and intercept and absorb more water, and larger plants trap or absorb more pollution from water. For water flow regulation, 41 out of the 60 studies reviewed focus mainly on the role of habitat area, typically in 'paired catchment' studies which compare two similar catchments with different forest cover, or the same catchment before and after felling. For atmospheric regulation and water quality regulation, a wider range of habitat and species attributes are found to play a role, including above and below-ground biomass, stand age, species size, stem density, successional stage, growth rate and wood density.

For air quality regulation and mass flow regulation (erosion control), the pattern is slightly different. Habitat attributes are still influential, with the area covered by vegetation being crucial, but so are species characteristics. Many studies compare different species of tree, shrub or herbaceous plants to determine which perform best for stabilising eroded slopes or trapping air pollution. For mass flow regulation, functional characteristics such as root depth, strength, density and structure are often found to be important for binding soil particles together and increasing soil infiltration (e.g. de Baets et al., 2009; Pohl et al., 2012). The structure, strength and elasticity of the above-ground vegetation is also important for intercepting rainfall, resisting water flow and trapping sediment, and the thickness and quality of the litter layer plays a key role in improving soil structure and protecting the soil surface from erosion (e.g. Andry et al., 2007). For air quality regulation, species characteristics such as leaf size, shape (needle or broad-leaved), stickiness and hairiness are also often investigated. Most articles conclude that coniferous trees are more effective at trapping pollution because their needle-shaped leaves have a high surface area, and because they are mainly evergreens and therefore can contribute to air quality all year round (e.g. Tallis et al., 2011). However, they may not be tolerant of high roadside pollution levels and salt from road run-off, so might not be appropriate for the 'front-line' positions immediately next to busy roads (Saebo et al., 2012).

Physical and biological diversity can enhance three of these services: carbon storage, water quality regulation and mass flow regulation. This is typically related to resource-use complementarity, where more diverse assemblages (e.g. with a range of canopy heights, root depths or photosynthetic responses) are more productive because they can exploit more of the available resources such as nutrients, water and sunlight (e.g. Cadotte, 2013; Cardinale et al., 2011; Lang'at et al. 2013). As these services tend to improve with the amount of biomass, a more productive ecosystem will tend to provide a better service. However, sometimes a less diverse mix of high-performing species (e.g. large trees for carbon storage, or pollution-tolerant reeds for water quality regulation) can be more productive or provide a better service (e.g. Ahmad et al., 2014; Cavanaugh et al., 2014). In contrast, diversity is rarely mentioned for air quality regulation, and water flow regulation is the only service for which no biological diversity attributes are studied in the literature reviewed. However, physical diversity in the form of structural complexity ('roughness') is found to increase protection against storm surges in coastal vegetation (Mazda et al., 1997; Ferrario et al., 2014) and to increase floodwater retention in floodplain woodlands (Thomas and Nisbet, 2006).

Most of the links cited in the literature have a beneficial effect, but three studies find that species abundance has a negative impact on flood protection as a result of invasive species (mangrove, willow or tamarisk) reducing river channel capacity and trapping sediment (Lee and Shih, 2004; Erskine and Webb, 2003; Zavaleta, 2000).

For the abiotic factors, the pattern varies considerably. Although rarely mentioned for carbon storage and water quality regulation, they are found to play an important role in the other services. Precipitation and slope have a direct negative impact on flood protection and mass flow regulation, as most erosion occurs during extreme rainfall events and on steep slopes. However, water availability has a beneficial impact as water is necessary for vegetation to become established, thus stabilising and protecting the slope. Drought conditions therefore often lead to more intense soil erosion. For air quality regulation the impacts of abiotic factors are complex and context-dependent. Wind can have a beneficial effect locally by dispersing pollution away from city streets or increasing deposition rates on leaves, but it can also re-suspend deposited particles (Nowak et al., 2006). High temperatures can decrease uptake of pollutants by plants (Alonso et al., 2011) and may also have a negative impact because certain tree species emit biogenic volatile organic compounds (B-VOCs) such as isoprene in hot weather, and these react with nitrogen oxides from traffic to form ground-level ozone pollution (Salmond et al., 2013). However, there can also be a beneficial effect in the range where warmer temperatures enhance plant growth, thus increasing the amount of vegetation that can trap pollutants.

3.1.2 Pollination and pest control

For pollination and pest regulation (Figures S8 and S9), studies tend to focus on the presence and abundance of the particular species or functional groups such as bees, butterflies, beetles, wasps or bats that provide the service. Species behaviour, i.e. flower-visiting or pest predation traits, is often cited as being important. For example, traits such as foraging distance, flight range, pollinator size and bee tongue length determine which pollinators can access certain flowers (e.g. Bommarco et al., 2011). Diversity (species richness) is also found to be important because a mix of pollinators of different shapes and sizes can provide a better landscape-level pollination service, and a mix of pest predators can target a larger range of pests, or pests at different life cycle stages (e.g. Badano and Vergara, 2011; Casulo et al., 2013; Garibaldi et al., 2014; Hoehn et al., 2008; Munyuli, 2013).

However, these services generally could not exist without the presence of the surrounding natural or semi-natural habitat to support the species providing the service, especially by providing food and shelter to beneficial insects after crops have been harvested. Habitat area is often found to be positively linked to the services of pollination and pest control, and the provision of these services tends to decline as the distance to natural habitat increases (e.g. Carvalheiro et al., 2010; Garibaldi et al., 2011). More diverse habitats support higher abundance and diversity of beneficial species, so vegetation species richness, structural diversity and landscape diversity are correlated with pollination and pest regulation efficiency (e.g. Daghela Bisseleua et al., 2013; Holzschuh et al., 2012; Rusch et al., 2013). The impact of abiotic factors on these services is rarely studied.

3.1.3 Food crops, fish and timber provision

For provision of fish, timber and food crops (Figures S10, S11 and S12), the service depends strongly on the existence of particular species that have favourable characteristics, such as palatability for food crops and fish, or straight growth habits for timber, as well as ease of cultivation. However, diversity also plays an important role: species richness is the most frequently cited attribute for food and timber production. This is not richness in the familiar sense of a diverse natural ecosystem (and indeed the term richness is not generally used in the literature reviewed), but the use of a relatively small number of species in practices such as intercropping and crop rotation for food crops, and mixed-species plantations for timber production. The principle is that co-production of species that exploit different resource niches can maximise yield. This is also observed for freshwater fishing, both in natural ecosystems and in aquaculture ponds or managed lakes stocked with mixed species of fish (e.g. Carey and Wahl, 2011; Lapointe et al., 2014; Rahman et al., 2008; Schindler et al., 2010). For food crops, intra-species genetic diversity (e.g. growing cultivar mixes) is often found to improve productivity or resilience; this is classified as species population diversity in our review.

For food crops, the benefit of diversity is often linked to co-cultivation with a leguminous crop that fixes nitrogen from the air, indicated by the attribute of 'Leaf N content'. For example, Smith et al. (2008) find that corn yields are over 100% higher with a three crop rotation including soy. However, negative impacts of crop diversity can arise due to competition for resources. Bayala et al. (2012) find that alley cropping grain with some tree species in the West

African drylands causes a decrease in yield due to shading, but using the *Faidherbia albidia* tree improves average yield because this species sheds its leaves during the rainy season.

Although polycultures and cultivar mixes often out-perform monocultures, there are also cases where the presence of a particular high-performing species or variety is cited as being important. For example, Cowger and Weisz (2008) find that it is necessary to include at least one high-yielding variety in wheat cultivar blends in the eastern USA. For food crop production, 48 out of the 60 studies find positive impacts of diversity, four find mixed impacts, five find unclear impacts and only one finds purely negative effects (Schroth and Lehmann, 1995, in their study of alley-cropped maize). The other two studies do not examine the impact of diversity. For timber production, 35 studies find that polycultures out-yield monocultures but five studies find the opposite.

Diversity is also cited as playing an important role in improving resistance to pests and diseases, and providing resilience to changing climatic conditions. For example, Hauggaard-Nielsen et al. (2008) find that intercropping legumes and barley reduces the incidence of barley disease by 20–40% compared to sole-cropping, and also suppresses weeds. Enhanced crop diversity can boost populations of natural pest and weed seed predators (Liebman et al., 2013), and the improved robustness and productivity also allows the use of agrochemicals to be reduced, which decreases production costs and provides further environmental benefits (e.g. Davis et al., 2012; Smith et al., 2008; Zhu et al., 2000). Even if more diverse systems do not provide higher yields in the short term, they can provide stability to changing conditions and reduce risk to producers in the long term (Smithson and Lenne, 1996). The evidence applies not just to field-scale studies but also to agro-biodiversity at the landscape level. Chavas and di Falco (2012) estimate that regional-scale crop diversity in Ethiopia boosts the productivity of Teff, the staple grain, by 65%.

Abiotic factors are cited as having important impacts on yield for food, fish and timber provision. For food production, for example, nutrient availability and water availability have mainly positive impacts but temperature and precipitation can have either a positive or negative impact depending on the context; they may improve crop growth, but crops are also susceptible to extremes of heat or cold and to waterlogging and storm damage.

3.1.4 Water supply

Water supply (Figure S13) is more similar to the regulating services than to the other provisioning services discussed here, because it depends largely on the entire community/habitat area rather than on species characteristics. However, in contrast to the other ecosystem services, the impact of biotic attributes is often negative. Although the interception of rainwater and absorption of groundwater by forests is beneficial for flood protection, as described above, it can also reduce water supply, which can cause problems where water is scarce. Most (42 out of 60) of the articles reviewed describe the negative effects of forests on water supply in water-scarce countries such as Australia and South Africa, although these are typically timber plantations of fast-growing non-native species such as pine or eucalyptus. Community/habitat area, presence of a community/habitat (forest), and stand age all tend to have negative impacts, as older/larger trees use more water (e.g. Nosetto et al., 2005), although Cavaleri and Sack (2010) found that forests used more water at earlier successional stages due to faster growth. Similarly, higher stem density and higher sapwood area can increase water use (Kagawa et al., 2009), and harvesting and thinning are found to significantly increase runoff and therefore increase provision in many studies (e.g. Petheram et al., 2002; Sahin and Hall, 1996).

In natural forests, in contrast, seven studies find beneficial impacts on water supply, with four showing how cloud forests intercept water from the air (e.g. Gomez-Peralta et al. 2008, Brauman et al. 2010) and three showing how forests can increase water yield by improving infiltration and soil water storage capacity (e.g. Singh and Mishra, 2012). Some studies show that native forests consume less water than pine plantations (Rowe and Pearce, 1994; Komatsu et al., 2008).

For the abiotic factors the situation is largely reversed compared to the service of flood protection, with precipitation and water availability having positive impacts and evaporation (i.e. transpiration) negative impacts.

3.1.5 Cultural services

Species-based recreation and aesthetic landscapes were reviewed as examples of cultural services. These show very different relationships between natural capital attributes and the service delivered.

For species-based recreation (e.g. wildlife viewing, hunting or fishing) the most frequently cited biotic attributes are the presence and abundance of specific species (Figure S14). These include charismatic species such as whales and dolphins for marine eco-tourism; rare birds or large mammals such as lions, tigers and elephants for land-based eco-tourism; game species such as deer for hunting; and fish such as salmon and trout for recreational fishing. Species size or weight can be significant, with visitors, fishermen and hunters often expressing a preference for larger species such as sharks and lions. Species richness and diversity are also valued by visitors. For example, Lindsey et al. (2007) find that tourists in South Africa consider functional group diversity (in this case, the variety of large mammals) to be the most important feature of their wildlife viewing experience, and Ruiz-Frau et al. (2013) find that marine biodiversity is important for scuba divers. Clearly the presence of suitable habitat to support the species of interest is important, but this is rarely addressed in the literature — possibly because many of the studies are set in protected areas where the existence of the supporting habitat may be taken for granted to some extent. There are five cases where species abundance is negatively linked to the service of species-based recreation (Table 1b) because, somewhat ironically, nature-watchers often place a higher value on rare species. Abiotic factors are rarely mentioned.

For aesthetic landscapes (Figure S15) the presence of a particular habitat is cited in 30 of the 60 papers, with forests and water features being most often mentioned, as well as urban trees and green space (e.g. Kaplan, 2007). Habitat structure is the most frequently cited attribute, with the term 'structure' being interpreted as covering a broad range of characteristics including landscape diversity and complexity, vegetation density, naturalness and uniqueness. Many studies find a preference for wilder, more complex, more natural landscapes (e.g. Acar and Sakici, 2008; Heyman, 2012; Daniel et al., 2012), especially in developed countries, but some cultural groups may prefer more open, managed landscapes with man-made elements. Abiotic attributes that are positively correlated with aesthetic appreciation are the presence of water (lakes and rivers) and steep slopes, which add interest and variety to the landscape.

3.2 Typology of links between natural capital attributes and ecosystem services

The information presented in section 3.1 and Table 1 enables identification of five pathways by which natural capital attributes influence the delivery of different bundles of ecosystem services (see Figure S17, Supplementary Material, for an indication of how the pathways are derived from the information in Table 1).

A. **Amount of vegetation**. The air, soil and water regulating services — air quality, atmospheric regulation, water flow, mass flow and water quality — are governed mainly by a group of biotic attributes related to the physical amount of vegetation within an ecosystem. These services all tend to improve as the vegetated area increases, or as the density of the above- and below-ground vegetation increases. Attributes such as community/habitat type and area, structure, stand age, successional stage, stem density and above- and below-ground biomass control the provision of these services. For the service of water supply, these attributes all tend to have a negative impact.
B. **Provision of supporting habitat**. For services that rely on particular animal species — pollination, pest regulation and freshwater fishing — the existence of suitable habitats to support those species is found to be important: natural or semi-natural habitats surrounding crops to support pollinators and predators after the crop is harvested, and suitable aquatic habitats with the right ecological, hydrological and climatic conditions to support fish through all stages of their life cycle. Community type, area and structure are therefore often

correlated with these services. It is likely that supporting habitat is equally important for the service of species-based recreation, but this does not emerge strongly in the literature reviewed. As a sub-division of this category, habitat type is also important for providing aesthetic value to humans.

C. **Presence of a particular species, functional group or trait**. The presence of particular species is found to be important for most services, especially species-based recreation and the provision of fish, timber and food. Specific functional groups are cited as being important for some services: these include groups of pollinators and pest predators such as bees and wasps, and also, for air quality and mass flow regulation, functional groups of plants such as large-leaved vs small-leaved trees or deep vs shallow-rooted shrubs. A range of species-specific attributes are positively correlated with service supply, including species size for fishing, species-based recreation and carbon storage; and species behaviour for pollination and pest regulation.
D. **Biological and physical diversity**. Biological diversity, reflected in the attributes of species and functional richness, functional diversity and (for food crops) intra-species population diversity, is often positively correlated with timber, food and fish production due to resource-use complementarity (section 3.1.1) or inter-species facilitation such as nitrogen fixation from the atmosphere by leguminous plants (section 3.1.3). Species richness is also often positively correlated with the service of pollination and (though reported to a lesser extent) pest control, as a mix of organisms with different characteristics (e.g. size, shape, flight patterns) can provide a more efficient service. Physical diversity is also often found to be significant, and this is reflected in the attributes of landscape diversity and, to a large extent, community or habitat structure, though the latter also includes other aspects of structure. More complex physical structures often provide a better service, e.g. a forest with a range of vegetation heights and root depths often provides more carbon storage; more diverse habitats provide better food and shelter for pollinating insects and pest predators; structural diversity enhances the aesthetic appeal of landscapes; and structural complexity tends to improve regulation of water flow and water quality.
E. **Abiotic factors** interact with the biotic attributes in complex and context-dependent ways, with much variation between services (Tables S1 and S2). Water supply appears to be particularly highly influenced by abiotic factors, with soil, precipitation and evaporation mentioned in over 70% of the articles reviewed. Food production is also dependent on a range of abiotic factors including nutrient availability, soil and precipitation. A number of services depend on water availability for establishment and survival of vegetation. In contrast, there is much less evidence on the influence of abiotic factors on pest regulation, species-based recreation and aesthetic landscapes.

These five pathways form the basis of a simple typology that describes the main ways in which different groups of biotic natural capital attributes influence the delivery of ecosystem services. **Error! Reference source not found.** summarises the typology, indicating the general direction of impact of each attribute group. Most attributes have a positive impact on service delivery, but the table also shows that mortality rate can have negative impacts, and that attributes in group A can have adverse impacts on water supply. For groups C and D the attributes are identified as having 'mainly positive' impacts on the bundles of services in the third column, to reflect the exceptions where certain (usually non-native) species have negative effects, e.g. introduced fish species wiping out native fish; or managed honeybees competing with wild pollinators. There are also some studies for food and timber production where diversity has a negative impact because a single high-performing species can provide a higher yield than a polyculture, at least in the short term.

Note that some attributes appear in more than one group:

- community/habitat type, area and age appear in groups A and B;
- community/habitat structure appears in group A (in terms of shape or form, such as patch size or connectivity) and in group D (in terms of structural complexity);
- species size and wood density appear in groups A (affecting the amount of vegetation) and C;

- population dynamics attributes (mortality rate, natality rate, life span/longevity and population growth rate) can affect biotic attributes in groups A to D.

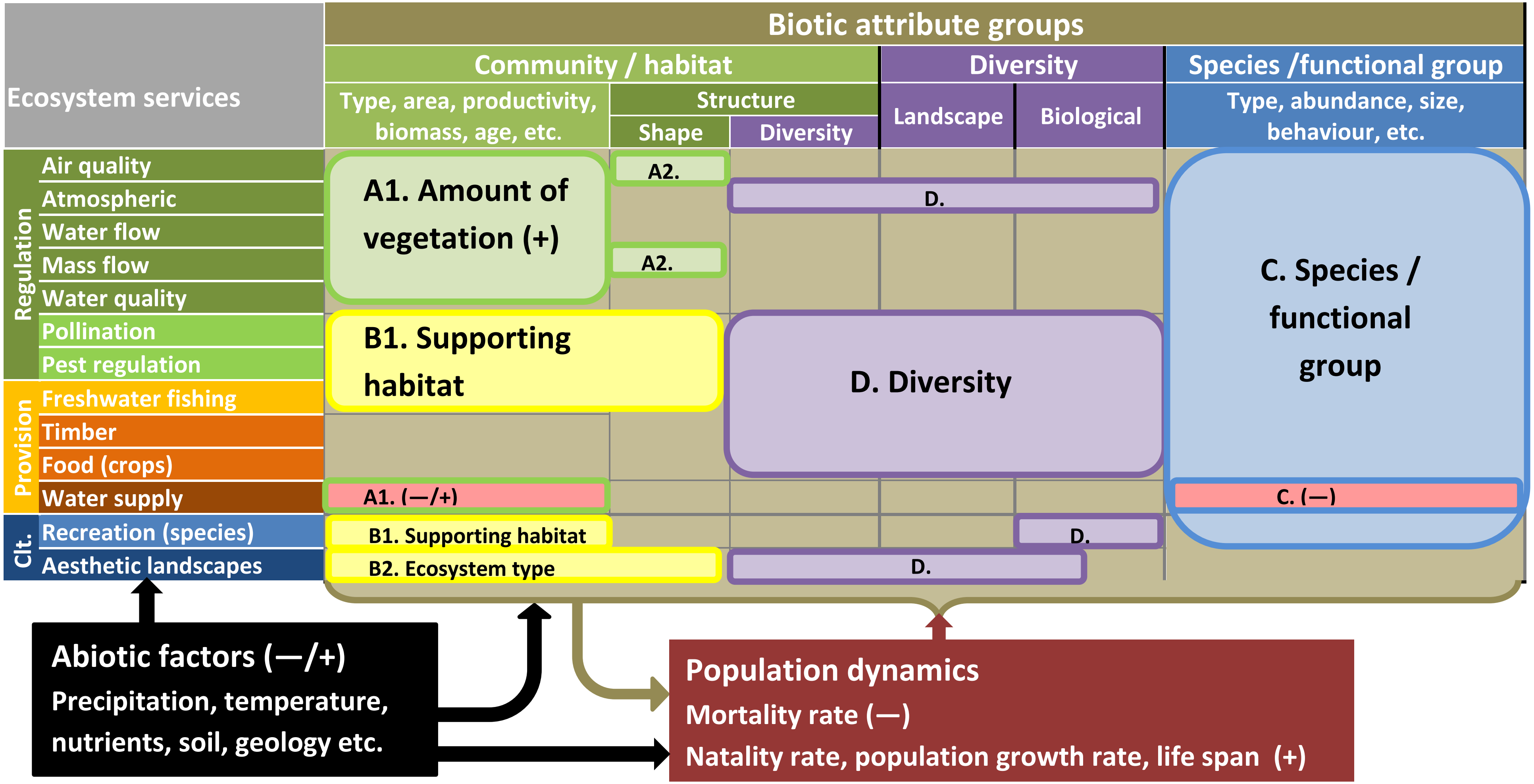
This grouping is not rigorous and there will be exceptions, such as in cases where invasive vegetation contributes to flooding by blocking river channels, so that the attributes in group A would have a negative impact on flood protection. Also, apparently weak links may indicate a lack of evidence rather than the absence of a causal link: for example there are no papers explicitly linking timber provision with plantation biomass, probably because the link is too obvious to merit investigation. Nevertheless, the typology provides a broad framework for classifying the pathways through which natural capital influences ecosystem services.

The typology is shown schematically in Figure 2, in which the population dynamics attributes have been separated from the main table to show how they can affect all the other attributes. The abiotic factors are shown as influencing the ecosystem services directly (e.g. through higher rainfall increasing water supply) and indirectly, through their impact on population dynamics which in turn affects all the other attributes. There is also a feedback loop to population dynamics from the other biotic attributes, because factors such as habitat area and the abundance of different species clearly influence population dynamics. Also, the attribute of community/habitat structure has been separated into two components: shape (classed as a sub-division of group A: A2) and structural diversity (part of group D). This distinction became apparent during the analysis but was not recorded in the database. Similarly, group B has been separated into two sub-divisions: B1 (supporting habitat for beneficial species) and B2 (aesthetic value to humans).

Table 2. Summary of typology to classify the pathways by which groups of natural capital attributes provide bundles of ecosystem services. Services for which there is more evidence for the influence of the pathway are highlighted in bold font.

Attribute group	Biotic attributes	Ecosystem services
A. Amount of vegetation	**Positive impact** + Presence of a specific community/habitat type + Community/habitat area + Aboveground biomass + Belowground biomass + Primary productivity + Community/habitat/stand age + Stem density + Successional stage + Litter/crop residue quality + Species size/weight + Wood density + Population growth rate + Natality rate **Negative impact** - Mortality rate	**Positive impact on:** + **Atmospheric regulation** + **Water flow regulation** + **Mass flow regulation** + **Water quality regulation** + **Air quality regulation** **Potentially negative impact on:** - **Water supply**
B. Provision of supporting habitat	**Positive impact** + Presence of a specific community/habitat type + Community/habitat area + Community/habitat structure	**Positive impact on:** + **Freshwater fishing** + **Pollination** + **Pest control** + **Aesthetic value**
C. Presence of a particular species, functional group or trait	**Positive impact** + Presence of a specific species type + Species abundance + Presence of a specific functional group + Abundance of a specific functional group + Flower-visiting behavioural traits (pollination) + Predator behavioural traits (biocontrol) + Sapwood amount + Wood density + Leaf N content + Species size/weight + Population growth rate + Life span/longevity + Natality rate **Negative impact** - Mortality rate	**Mainly positive impact on:** + **Freshwater fishing** + **Timber** + **Food production (crops)** + Air quality regulation + Atmospheric regulation + Mass flow regulation + Water quality regulation + **Pollination** + **Pest regulation** + **Species-based recreation**
D. Biological and physical diversity	**Positive impact** + Species richness + Species population diversity + Functional richness + Functional diversity + Landscape diversity + Community/habitat structure	**Mainly positive impact on:** + Freshwater fishing + **Timber** + **Food production (crops)** + Air quality regulation + **Atmospheric regulation** + Mass flow regulation + Water quality regulation + **Pollination** + Pest regulation + **Species-based recreation** + **Aesthetic landscapes**
E. Abiotic attributes	± Temperature ± Evaporation ± Wind ± Precipitation, snow ± Water availability ± Water quality ± Nutrient availability ± Soil, geology, slope	**Affect all services in context-specific ways**

Figure 2 Summary schematic diagram of pathways by which groups of natural capital attributes deliver bundles of ecosystem services



3.3 Interactions between services

Interactions between ecosystem services are mentioned in 40% of the articles reviewed. Most (56%) of the interactions identified are positive, highlighting the multiple benefits that particular ecosystems can provide (Figure 3). There are strong links between the bundle of air, soil and water regulating services and the cultural service of aesthetic landscapes, as these services are all underpinned by similar attribute groups (with a high contribution from A, amount of vegetation, and D, diversity), and thus are often provided by the same habitat type, with forests typically providing a high level of all these services. The links from air quality regulation to the other services in this bundle are particularly strong, as many studies cite the multiple benefits of urban trees in helping to improve air quality, reduce flood risk, store carbon and provide aesthetic value. Links from pollination and pest regulation to food crop production are also strong.

There are also some negative interactions between services, especially between provisioning services and regulating or cultural services, although these are mentioned less frequently. These negative interactions are usually linked to human management activities that benefit one service but at the same time have negative impacts on another. A strong negative link is evident between timber production and water supply: this refers to the impact of timber plantations on water supply in water-scarce regions. Timber and food crop production also have negative links with atmospheric and water flow regulation, arising from the decrease in these services when forests are felled for timber or cleared for agriculture. Cultivation of land for food crops can also exacerbate soil erosion, and fertiliser application benefits food and timber production but has negative impacts on water quality regulation and freshwater fishing. Some management activities may have short-term benefits but may result in adverse consequences in the long-term (such as a decline in pollinators and thus increased risks to food security due to intensive farming). Improved analysis of these interactions could help decision-makers to develop management strategies that exploit synergies and balance trade-offs more effectively.

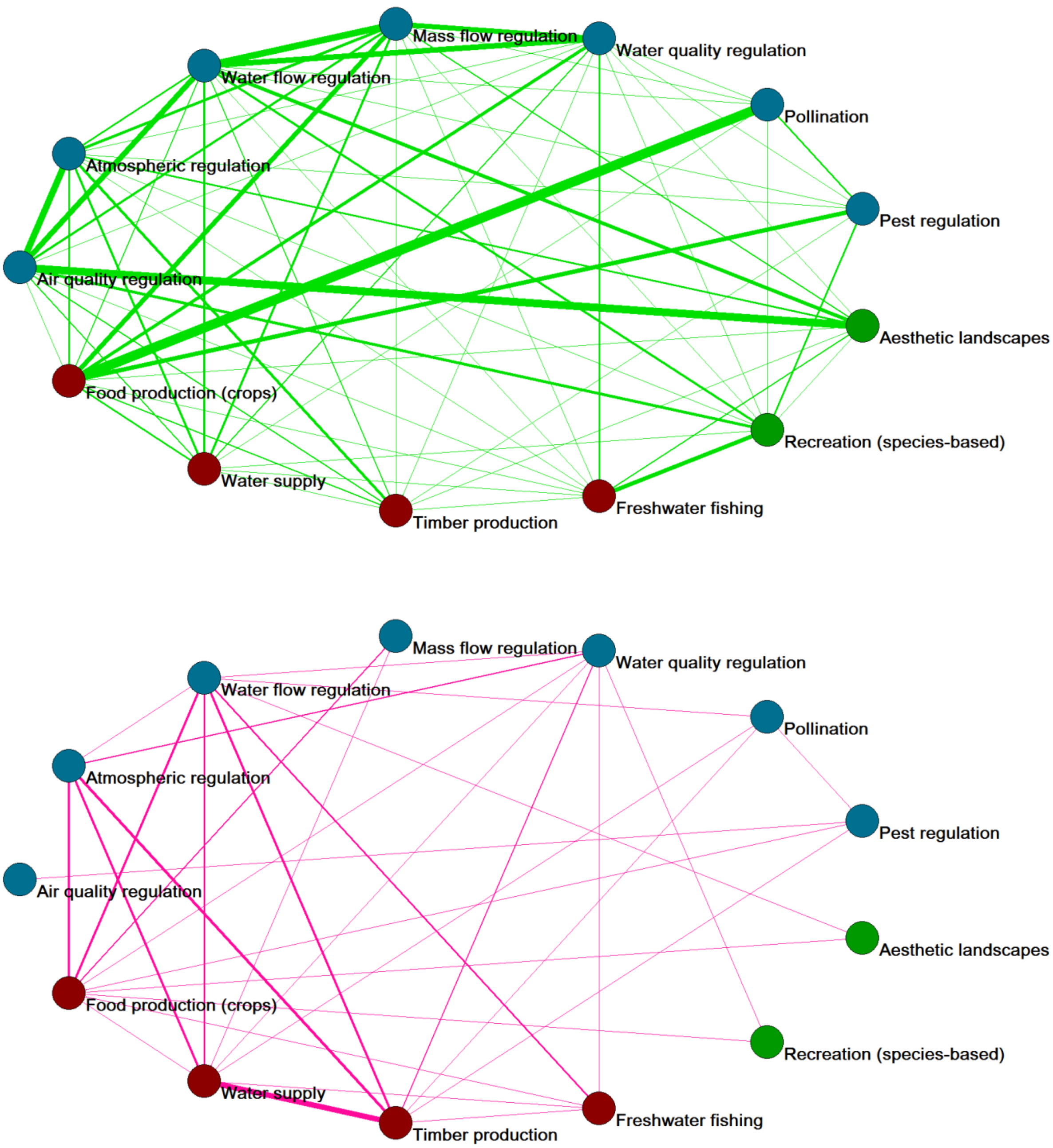


Figure 3. Network diagram showing all positive (top) and negative (bottom) interactions between services. Thickness of lines is proportional to number of studies supporting a link. Water flow regulation = flood protection; mass flow regulation = erosion protection.

3.4 Human impacts

Human activities are shown to have a range of positive (21%) and negative (15%) impacts on ecosystem service delivery, and 18% of studies cite a mix of both (Figure S19). This part of the review was expected to record any direct human input and management activities intended to boost the service (such as the use of fertilisers), but we found that it is far more common for the articles reviewed to cite impacts related to other human activities, some of which are related to other ecosystem services (and thus also covered under the 'Interactions' section above). Thus there are many examples in which ecosystems have been lost or damaged through urban development or over-exploitation, altering the functioning of the ecosystems and reducing some of the services they deliver. However, there are also many examples of ways in which protection, restoration and sustainable management of habitats can actively enhance ecosystem service delivery.

Although for most services we found a split between positive, negative and mixed impacts, for food crop and timber production no studies show purely negative human impacts on service delivery. This is because food crop production always requires a certain level of positive human input: sowing, tending and harvesting the crop. The same is true for timber production, as all the articles reviewed concern production from managed or experimental plantations as opposed to felling of unmanaged forest. For freshwater fishing, many of the studies cover managed systems where beneficial human activity includes stocking and sometimes feeding the fish (e.g. Boukal et al., 2012), but negative impacts also arise from over-fishing or habitat degradation, e.g. through pollution, dredging, deforestation or dam construction (e.g. Dugan et al., 2010; Hoeinghaus et al., 2009). Air quality regulation is the only other service where human impacts are cited as being largely positive, reflecting the need for active management of urban vegetation.

Careful regulation and sustainable management, along with protection of key habitats, offers opportunities to maximise the delivery of multiple ecosystem services and avoid over-exploitation. For mass flow regulation, for example, 37 out of 60 papers cite negative (or mixed positive and negative) human impacts, mainly from overgrazing or intensive cultivation of arable land, though also from fuelwood collection, ski-run construction and road building (e.g. Garcia Nacinovic et al., 2014; Liu et al., 2014; Pohl et al., 2012). However, 20 of these papers show how impacts could be mitigated through restoration and soil-water conservation methods such as re-planting or re-seeding with protective vegetation, constructing low walls or terraces on steep slopes, establishing contour hedges or grass buffer strips between fields, using cover crops to avoid bare soil in winter, and shifting to no-till agriculture (e.g. Gao et al., 2011; Liu et al., 2014; Munro et al., 2008). For pest regulation and pollination, adverse impacts are recorded from clearance of natural habitats and over-use of agro-chemicals, but there is also considerable evidence of benefits from shifting to organic agriculture and establishing supporting habitat, e.g. at field margins (e.g. Colloff et al., 2013; Munyuli et al., 2013; Watson et al., 2011). For species-based recreation, many of the studies are set in protected areas with active conservation policies, but monitoring and regulation (such as limiting the size of tour groups) is also often found to be necessary to avoid damage or disturbance to species from tourist activities (e.g. Zhang et al., 2012). Deforestation has a severe impact on carbon storage and flood protection, but several studies highlight the benefits of protecting or restoring forested areas (e.g. Gonzalez et al., 2014; Ogden et al., 2013).

4 Discussion

4.1 Comparison with other studies

Our systematic review built a coherent database recording the direction of links between natural capital attributes and ecosystem services, based on the number of papers presenting evidence for each link. Previous studies of the links between ecosystem services and natural capital have often been based only on one attribute — usually species richness — or have investigated a limited range of ecosystem services (Cimon-Morin et al., 2013; Duncan et al., 2015). By including 29 biotic attributes, 11 abiotic factors and 13 ecosystem services in our analysis, we have been able to examine not just the impact of diversity but also the influence of attributes related to specific habitats, species and functional groups. This enables a comprehensive overview of the pathways by which natural capital contributes to ecosystem services, which underpins the typology we developed. However it is important to note that this is a vote-counting approach and not a meta-analysis. The number of papers citing a positive or negative link is not proportional to the importance or strength of that link. Similarly, the absence of evidence for a link does not necessarily mean that the link does not exist, but only that evidence for it has not been reported in the literature.

This review extends the knowledge base compiled by Harrison et al. (2014). We add information on the direction of influence of abiotic factors, thus providing a more complete picture of the way in which both biotic and abiotic elements of natural capital interact to deliver ecosystem services. This review also adds two more ecosystem services and 250 recent papers, as well as collecting information on interactions between services and human impacts. A detailed comparison with Harrison et al. (2014) shows that the net direction of the links between biotic attributes and ecosystem services is the same for all attributes, but our new review finds stronger evidence for a number of links, including:

- the positive role of the set of attributes related to the amount of vegetation (habitat area, above- and belowground biomass, stem density, growth rate, primary productivity, successional stage, stand age, species size and wood density) in the provision of services of atmospheric regulation, mass flow and water flow regulation;
- the importance of the area of supporting habitat to underpin the species-related services of pollination, pest control and freshwater fishing;
- the role of species richness and functional diversity in boosting timber production and pollination;
- the role of species behaviour in providing pollination and pest control;
- the importance of habitat structure (including structural diversity) in enhancing the services of pollination, pest control, mass flow and water flow regulation.

The new typology offers several advantages over the one developed by Harrison et al. (2014), which was structured around Ecosystem Service Providers (ESPs), which are the species, functional groups or communities/habitats that provide services (see Supplementary Material Section 2 and Figure S16). One problem is that ESPs are rarely explicitly identified in the literature and have to be inferred by the reviewer, leading to some potential for inconsistency. Also they are often determined mainly by the study design (i.e. whether the researchers choose to investigate the role of one or more species, functional groups or entire habitats), rather than reflecting the ecosystem components required to provide the service. And finally, although the network diagrams linking services to ESPs and attributes are very effective in illustrating the complexity of the links that underpin different services, they cannot easily be used to inform management decisions. The new typology presented here offers a simpler way to trace the pathways by which natural capital provides ecosystem services, and links the delivery of ecosystem services more clearly with the ecosystem functions that underpin them.

This review has helped to improve understanding of the links between ecosystem functions and ecosystem services – a research gap that has been noted by several reviews (Cardinale et al., 2012; Duncan et al., 2015; Wong et al., 2015). The biotic attribute groups (A to D) have parallels with the groups of ecosystem functions that Duncan et al. (2015) identify as underpinning bundles of ecosystem services. For example, Duncan et al. (2015) note that the service of mass flow regulation is underpinned by a group of ecosystem functions including Net Primary Productivity, below-ground biomass and soil texture — equivalent to several of the attributes identified in our typology. The breadth of the literature covered by our systematic review enables us to provide a complete typology in line with this framework.

Our findings are also broadly in line with two studies that use spatial correlations between ecosystem service proxy indicators (such as water quality, agricultural production or tourism) to identify ecosystem service bundles. Maes et al. (2012) identify a bundle of ecosystem services spatially correlated with forests, including air quality regulation, carbon storage and erosion protection, in line with group A in our typology, as well as recreation and timber production. Rausdepp-Hearne et al. (2010) identify a similar 'Country homes' bundle located in undeveloped forests that includes carbon storage, soil organic matter and water quality (similar to group A) as well as recreation. Both these studies also identify trade-offs between the provisioning services (especially food production) and the regulating and cultural services, in agreement with our findings (section 3.3).

Our typology is also consistent with the framework proposed by Maseyk et al. (2017), who identify three ecological processes that underpin ecosystem services: the species-area relationship (equivalent to our group C, specific species; and B, supporting habitat); landscape ecology (group D, physical and biological diversity); and biodiversity-ecosystem function (group D, biological diversity). However our typology also identifies group A – amount of vegetation.

4.2 Implications for ecosystem management

The database identifies the structural and functional factors (natural capital attributes) that link natural capital stocks to ecosystem service flows in different contexts, thus increasing understanding of the biophysical control of ecosystem services. This can be used to inform sustainable ecosystem management. Here we address three issues: the impact of ecosystem condition on service delivery; the compatibility of the ecosystem service approach with conservation objectives; and how the typology can be used to inform management decisions in practice.

4.2.1 Ecosystem condition and thresholds

As part of the review, we aimed to gather any information on the condition of ecosystems and to evaluate the feasibility of detecting possible thresholds beyond which service delivery would be compromised. However, very few studies explicitly mentioned either ecosystem condition or thresholds. One exception was for the service of flood protection, where several papers cited a threshold effect where storm flows increase noticeably when forest cover in the catchment falls below 20-30% (Bathurst et al., 2011; Lin & Wei, 2008; Schnorbus & Alila, 2013).

As an alternative, we propose that many of the natural capital attributes in our typology could be used as indicators of ecosystem condition. This could include the area of different habitats, biological and physical diversity attributes, the presence and abundance of specific species and functional groups (including undesirable species such as pests or invasive species), population dynamics attributes such as natality, mortality and growth rates, and abiotic indicators such as water quality and water availability. The typology enables these attributes to be linked to the services that depend on them.

4.2.2 Compatibility of the ecosystem services approach with conservation objectives

The findings of this review may help to inform the debate over whether the ecosystem service concept is compatible with conservation objectives. In particular, it highlights the role of biological and physical diversity in delivering many ecosystem services. Diversity can increase productivity through at least three mechanisms: resource-use complementarity (see section 3.1.1); the selection or sampling effect, where the presence of a greater number of species increases the chances that some of them will be good providers of a particular ecosystem service (Cavanaugh et al., 2014); and inter-species facilitation such as nitrogen fixation from the atmosphere by leguminous plants (Hulvey et al., 2013). More recently, van der Plas et al. (2016) have proposed the existence of an additional mechanism which they term the 'Jack-of-all-trades' effect, caused by the averaging of individual species contributions to ecosystem functions.

Our review finds that diversity can enhance the delivery not only of regulating and cultural services, but also provisioning services. For food, timber and fish provision, more diverse systems often provide higher yields in the short term, as well as greater yield stability in the long term. Although diversity in managed systems is far more limited than within natural ecosystems, it can still offer benefits for wildlife when compared to a monoculture, for example through a mosaic landscape that offers a mix of species and cultivars both within and across fields, coupled with networks of natural or semi-natural habitats to support pollinators and pest predators (Scherr and McNeely, 2008). Increased diversity can also enhance resistance to pests and diseases and reduce the need for agro-chemical inputs, which brings further ecosystem benefits (see Section 3.1.3). Although there is a conflict between forests and water supply, this mainly applies to monocultures of non-native species such as pine or eucalyptus, and there is evidence that biodiverse native forests have lower impacts or even benefits (see Section 3.1.4 and also more recent work e.g. Carvalho-Santos et al., 2016).

For the regulating and cultural services reviewed, the strength of the relationship between diversity and ecosystem service delivery is often context-dependent, which may explain why there is not always a good spatial correlation between biodiversity and ecosystem service delivery (Cimon-Morin et al., 2013). For example, the studies on carbon storage reveal that the relationship may depend on the scale of the study, the structural complexity of the forest (Tran van Con et al., 2013), the productivity of the site (Potter and Woodall, 2014) or the successional stage (Gonzalez et al., 2014) (see Supplementary Material section 2.1.1). The nature of the study may also have an impact. Ricketts et al. (2016) review 81 studies for four ecosystem services (carbon storage, pest control, pollination and water purification) and find that the strength of biodiversity-ES relationships varied depending on whether the studies focused on spatial correlations between biodiversity and ES, the impact of management interventions, or the functional mechanisms by which biodiversity affects ES. It would be useful to investigate these issues in further work.

Despite this evidence on the positive links between diversity and ecosystem services, there are still a number of potential conflicts. Firstly, the information collected on human impacts confirms that over-exploitation of provisioning services, and sometimes cultural services (e.g. tourism), often has negative impacts on ecosystems. Secondly, the review highlights that forests have a particular value in providing multiple ecosystem services, but over-emphasis on protecting forests could lead to loss of other ecosystems such as heathland, natural grasslands or sparsely vegetated land that provide fewer regulating services but may still be home to rare or threatened species and have cultural value. Thirdly, species richness may reach a plateau beyond which service delivery does not increase (Balvanera 2006; Chen, 2006). This means that there may be no incentive to restore or protect the richest ecosystems, as moderately rich systems such as managed plantations with three or four timber species could provide the same level of service (Cardinale et al., 2006; Ingram et al., 2012). Fourthly, some services may be delivered adequately by relatively common species (Ridder, 2008) or by non-native species such as managed honeybees, which have little conservation interest or may even have negative impacts through competition with native species (Paini and Roberts, 2005).

To resolve these potential conflicts it is necessary to ensure that the ecosystem service concept is applied within a holistic management framework that balances stakeholder demands for a wide range of provisioning, regulating and cultural services, and aims to maintain resilient ecosystems that can deliver a sustainable supply of services in the long term (Haslett et al., 2010; Macfadyen et al., 2012; Smith et al., 2016). Synergies with conservation goals can be improved by ensuring that due weight is given to cultural ecosystem services, such as eco-tourism or the existence value of wildlife, and highlighting their links to the attributes of ecosystems (Blicharska et al., 2017; Reyers et al., 2012). Short-term over-exploitation of specific services is not compatible with a sustainable ecosystem service management approach. The review highlights the vulnerability of ecosystems to changing abiotic factors such as temperature and precipitation, especially for the provisioning services, and provides evidence for the role of diversity in providing resilience to climate change, particularly for production of food crops (e.g. di Falco and Chavas, 2008).

There is ample evidence that diversity is necessary to ensure that ecosystems are multifunctional and that they are stable over time under changing environmental conditions, reducing risks to the service beneficiary (Cardinale et al., 2012; Duncan et al., 2015; Isbell et al., 2011; Lefcheck et al., 2015). This shows that maintaining diverse and healthy ecosystems is fundamental both to conservation goals and sustainable ecosystem service delivery.

Despite the opportunities for synergies between ecosystem services and biodiversity conservation, win-wins can be hard to achieve in practice and trade-offs must be explicitly tackled (McShane et al., 2011). For example, Barnett et al. (2016) found trade-offs between reforestation to improve water quality (focusing on riparian buffers) and reforestation to connect black bear habitats. Joint management of biodiversity and ecosystem services (Cordingley et al., 2016; Reyers et al., 2012) coupled with appropriate regulation (Albert et al., 2016) is needed to minimise trade-offs and avoid adverse impacts.

4.2.3 Informing management decisions

This review provides an extensive evidence base that can be used to demonstrate the value of natural capital to decision-makers. Our typology of links between natural capital and ecosystem service delivery can help to guide the application of the ecosystem service approach in research, policy and practice for sustainable land, water and urban management.

The typology is not intended to cover every aspect of ecosystem service delivery, and it has already been noted that there can be exceptions to the broad classifications, as many of the links are context-dependent. Nevertheless, it is intended to be a clear and simple classification that can be used by land managers and other decision makers to raise awareness of the different pathways by which natural capital attributes affect ecosystem service delivery. Selected attributes can be used as biophysical indicators for monitoring and managing ecosystems. A manager might then be able to estimate the impact of a land management action on different bundles of ecosystem services. One approach that has already been applied in practice is to use the typology as a basis for a simple land-use scoring approach to mapping the ability of different habitats to provide different ecosystem services (Smith and Dunford, 2017).

The studies reviewed contain many examples of successful initiatives to restore degraded ecosystems and manage services more sustainably (section 3.4). To assist with this, Maseyk et al. (2017) suggested dividing the attributes of natural capital (soils and vegetation) into manageable and unmanageable attributes, so that management strategies can focus on the manageable attributes. The review of potential interactions between services (Section 3.3) can help to inform the development of management strategies to maximise synergies and minimise undesirable trade-offs.

5 Conclusions

This review has compiled a significant evidence base of 780 papers that demonstrates the ways in which different elements of natural capital influence the delivery of ecosystem services. This has been used to develop a simple typology that defines five groups of attributes that support specific bundles of services in different ways: A) the physical amount of vegetation cover; B) presence of suitable habitat to support specific species or functional groups that provide a service; C) the characteristics of particular species or functional groups; D) physical and biological diversity; and E) abiotic factors. This provides a consistent framework to inform further research, analysis and decision-making.

The evidence base can be used to demonstrate the value of natural capital, and can thus support decisions to protect, restore or enhance ecosystems in order to ensure the long-term provision of the range of services needed to underpin human wellbeing. We have also provided an overview of positive and negative interactions between services, and evidence on the impact of human management on service delivery. This can be used to identify opportunities to gain multiple ecosystem service benefits, and also to recognise situations where there could be trade-offs between ecosystem services, and determine suitable management actions to avoid or mitigate any problems. Finally, the review provides evidence on the value of physical and biological diversity both in enhancing short-term performance and underpinning the long-term resilience of ecosystem services to environmental change. This shows that the ecosystem approach, if applied correctly, can provide additional motivation to conserve healthy, diverse ecosystems that simultaneously deliver services for people and habitat for wildlife. The review thus supports the objectives of the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES) by providing pertinent evidence for the conservation and sustainable use of biodiversity, long-term human well-being and sustainable development.

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