Introduction

The well-being of society depends to a large extent on the benefits derived from the functions and processes that take place within ecosystems (i.e., ecosystem services). Biodiversity plays an important role in the delivery of many of these benefits. However, human activities that derive services from ecosystems may also have adverse impacts on ecosystems and their biodiversity. This can negatively impact societal well-being, if degradation of biodiversity results in a decline in the quantity, quality, or resilience of ecosystem service provision. Understanding how biodiversity is linked to ecosystem services is critical for designing more sustainable environmental policies and landscape planning.

The significance of declines in biodiversity and the consequences for ecosystem services are increasingly being recognized. For instance, the over-exploitation of fish stocks has led to declines in marine biodiversity via by-catch and fisheries collapse (Worm et al., 2006). Declines in numbers and diversity of wild insect pollinators have been linked to changes in fruit set for many highly valuable crops (Luck et al., 2009). In the absence of effective management, the effects of declining biodiversity and ecosystem degradation will be exacerbated by climate change, with consequences especially for the well-being of future generations.

In this chapter, we first examine key concepts that are relevant to understanding the links between biodiversity and ecosystem services. We then review the relationship between biodiversity and ecosystem services, as well as the complexities arising from such linkages. We then provide an in-depth description of the links between biodiversity and several critical services, provided through different mechanisms and at different scales. Finally, we conclude by offering some new perspectives on addressing the links between biodiversity and ecosystem services and outline the challenges that lie ahead in this area.
Key concepts relevant to understanding the links between biodiversity and ecosystem services

Different facets of the biodiversity link to ecosystem services

Biodiversity broadly encompasses the number, abundances, functional variety, spatial distribution, and interactions of genotypes, species, populations, communities, and ecosystems. What levels of organization or components of biodiversity are likely to be most strongly linked with ecosystem services? For plant-dependent services, the local number of functional groups and total number of species (richness) can offer a crude first-order prediction for several ecosystem processes, such as productivity, and services, such as forage production. For animal-dependent services, species number and composition in mammalian communities are associated with regulation of infectious disease, although the direction of this effect (amplification or dilution of disease) depends on the types and relative abundance of different vector species in the community (Ostfeld and Keesing, 2012). The equity of the abundances (evenness) of individual species is also important in relation to biological invasions. For example, reducing evenness in plant species communities can decrease resistance to invasion by exotic plants and insect herbivores (Wilsey and Polley, 2002).

Theory predicts that increasing horizontal diversity (numbers of species within trophic levels) tends to promote several ecosystem functions that feed into ecosystem services; however, increasing vertical diversity (numbers of trophic levels) does not necessarily do so (Loreau, 2010). For plant-dependent ecosystem services, the level of service delivery probably depends most on local plant diversity because plant species interact at a local spatial scale, but there is some evidence that ecosystem services could depend on plant diversity at larger spatial scales (beta or gamma diversity; Isbell et al., 2011).

The different components of ecosystem services

A critical issue in ecosystem service assessments is the scant knowledge on how ecosystem services and their components (i.e., supply, delivery, use demand, value and benefits) are produced and maintained, how they are affected by system changes, such as land use change, and how they depend on different levels of biodiversity. To improve this knowledge, we distinguish between ecological processes (called ‘supporting services’ in the Millennium Ecosystem Assessment; MA, 2005) and ‘functions’ that produce ecosystem services. Functions are intermediate products; they are necessary to the production of services but are not services themselves, i.e., not used or acknowledged directly by a beneficiary. These intermediate products or processes often underpin or determine the potential service production or supply, which can benefit society. The delivery of a service arises from the interaction between its supply and the demand from stakeholders who benefit from it (Tallis et al., 2012). The benefit and value of a service reflect how people assign importance to the service, which can be evaluated in terms of market value or from a cultural perspective. For example, primary production (an ecosystem process) is needed to maintain abundance of fish population (the service supply), which can be harvested to provide food (delivery) and high nutritional value (benefit). As another example, nutrient cycling (process) is needed for water purification (supply) to provide clean water (delivery) for domestic use (benefit) (Raffaelli, 2016; Jax, 2016a).
Useful concepts for assessing the links between biodiversity and ecosystem services

To analyse the influence of biodiversity on ecosystem functions and service delivery in a structured manner, the concept of ecosystem service provider (ESP) can be useful. An ‘ESP’ only relates to specific organisms (from vascular plants, vertebrates to microbes) and variation of their attributes (e.g., genetic diversity, species diversity, species richness, functional diversity and vertical diversity) (Luck et al., 2009, see also Luck, 2016). These ESPs can then be linked to service supply and to the needs of beneficiaries (Jax, 2016b).

The concept of functional trait can also help elucidate links between biodiversity and services. Trait-based approaches can be used to understand how species contribute to multiple ecosystem functions and also to investigate the mechanisms that contribute to trade-offs among ecosystem services.

Recently, two other concepts have been suggested in the context of the trait-based ecosystem service approach (Diaz et al., 2013): the Specific Effect Function (SEF), which is the per unit capacity of a species to influence an ecosystem property or service; and the Specific Response Function (SRF), which is the ability of a species to maintain or enhance ecosystem services quantity in response to a specified change in the abiotic or biotic environment or to invade environment afresh.

Linking biodiversity to different types of services

Although the classification of ecosystem services proposed in the Millennium Ecosystem Assessment (MA, 2005) is widely adopted, there have been many other frameworks that aim to make the classification more relevant to decision-makers, economists, and ecologists. In fact, different classifications may be useful for different purposes.

The main challenge is that the same component of biodiversity may be linked in very different ways to multiple ecosystem services. Fish provide a good example. Fish are widely recognized as food, a ‘provisioning service’ with a direct market value. However, fish also provide indirect benefits or regulating services, like biological control. Specifically, experiments have highlighted the importance of fish predation in regulating invasive species like zebra mussels. Concurrently, the presence of fish, such as in crowded streams during spawning, can also be a highly valued cultural service.

Biodiversity and magnitude of provisioning and regulating services

The evidence to date

Our evidence that provisioning and regulating services depend directly on biodiversity remains limited. We suspect that this lack of evidence is likely due to a lack of adequate testing, rather than a lack of dependence. For ecosystem functions, hundreds of field experiments (reviewed by Cardinale et al., 2011) and dozens of theoretical studies (reviewed by Loreau, 2010) have established that decreasing plant diversity can alter ecosystem functioning in directions that would likely reduce ecosystem services. They have rarely, however, tested the direct dependence of final ecosystem services, such as fodder production, on biodiversity (Balvanera et al., 2014).
Possible mechanisms

Why might provisioning and regulating ecosystem services depend on biodiversity? There are three main ways in which increased biodiversity may result in increased ecosystem service provision and hence explain why decreasing biodiversity could lead to a decrease in ecosystem services.

First, complementary differences between species, combined with spatial heterogeneity, could lead to the whole community providing services at rates greater than the sum provided by its component species. This is currently referred to as the complementarity effect (Loreau and Hector, 2001).

Second, dominance by species that provide particularly high rates of ecosystem services could lead to a positive diversity effect on the provision of ecosystem services, on average. However, in this case, the community would never outperform the single best species that it contained. This is currently referred to as the selection effect (Loreau and Hector, 2001).

Third, asynchronous responses of species to environmental fluctuations could lead to greater and more stable provision of ecosystem services in mixtures than in monocultures. This is currently referred to as the insurance hypothesis (Yachi and Loreau, 1999).

The shape of the relationship between biodiversity and services

It is becoming increasingly clear that even the loss of a few species from a diverse community could have an adverse impact on ecosystem functioning and services. Before biodiversity experiments were conducted, most investigators predicted that ecosystem functioning would saturate at relatively low levels of biodiversity. This redundancy hypothesis posited that most species are functionally redundant, and thus their loss would not impact ecosystem functioning. Dozens of field experiments seemed to confirm this prediction (Cardinale et al., 2011).

However, diversity effects tend to increase over time in long-term experiments. More importantly, the relationship between biodiversity and ecosystem functioning becomes increasingly linear over time. Thus, long-term studies tend to indicate that even the loss of a few species from diverse communities could have large impacts on ecosystem services, while results from short-term studies tend to suggest that most species are redundant.

Biodiversity and multiple services

Ecosystem services studies have often found trade-offs between ecosystem services as well as bundles, i.e., sets of different services that interact synergistically and occur simultaneously across landscapes provided by different land uses. Changes in biodiversity will likely lead to trade-offs in ecosystem service provision. For example, converting diverse grassland to cropland tends to provide high levels of crop production but low levels of many other ecosystem services. There is now considerable evidence that different ecosystem processes depend on different sets of plant species (Isbell et al., 2011). Furthermore, more diverse plant communities can provide higher levels of multifunctionality and higher levels of multiple ecosystem services.

The gaps

Uncertainty about the links between biodiversity and ecosystem services remains considerable (Balvanera et al., 2014). These uncertainties arise from: i) mismatches between ecosystem functions measured and final ecosystem services; ii) mismatches between study conditions and management conditions; iii) insufficient consideration of all functions upon which a service
depends; iv) insufficient integration of multiple potentially critical components of biodiversity; v) confounding environmental factors; vi) trade-offs between the positive and negative effects of changes in biodiversity on various ecosystem functions that underlie ecosystem services; vii) context-dependent patterns; and viii) different scales between studies linking biodiversity and both the management and delivery of services.

Biodiversity and cultural services

The evidence to date

Cultural services supply a broad spectrum of non-tangible and non-market benefits to human well-being (i.e., psychological health, social relationships, and cohesion). These non-material benefits obtained from biodiversity can be related to different types of values (e.g., moral, spiritual, or aesthetic values), which have different importance depending on social and institutional contexts or stakeholders’ groups (Chan et al., 2011; Chan and Satterfield, 2016; see also Landers et al., 2016). It follows that cultural services should be analysed considering the range of services (i.e., recreational activities and tourism, aesthetic values, spiritual values, local identity, etc.) and the range of values given to each service by individuals. These values are also at the very core of any decision relating to managing provisioning, or regulating services.

The different ways in which biodiversity and cultural services are linked

Differences in vegetation colour, often related to leaf nitrogen content, can be associated with the aesthetic value of landscapes. At the species level, functional traits of vegetation are significant for the supply of specific cultural services, such as recreation and aesthetics. For example, the variety of colours and green tones strongly relate to the landscape enjoyment of some ecosystems. In animals, physical traits such as large size and neotenic features (the retention of juvenile traits by adults) are important determinants of their aesthetic value.

At the level of ecosystems, recreational and aesthetic values have been attributed to those multifunctional landscapes with intermediate levels of biodiversity and some accessibility level. Multifunctional landscapes that are extensively managed have been shown to have high aesthetic and existence values (Garcia-Llorente et al., 2012). People prefer them, not only for aesthetic reasons, but also because they can provide a larger set of ecosystem services than landscapes that are intensively managed or abandoned.

Social preferences towards landscapes have been also linked to the presence of visible water and vegetation, specifically referred to as hydrophilia and phytophilia, respectively. At landscape scales, expert assessments have highlighted that vegetation diversity at the species and community levels are very important for the delivery of cultural services (Quijas et al., 2012).

The gaps

The analysis of the link between biodiversity and cultural services faces many scientific challenges. As has been reported for the UK (UK NEA, 2011), there is a ‘cultural divide’ in our knowledge because for those culturally important taxonomic groups (i.e., butterflies, fish, birds, mammals), there is high-quality information about their status and trends, but a knowledge gap on their associated cultural services (i.e., recreation, aesthetic values, existence values). In addition, for certain cultural services, such as local ecological knowledge, cultural heritage, or sense
of place, there is limited knowledge about the biodiversity components that act as ecosystem service providers, such as crop or livestock varieties, native plants, and autochthonous animal breeds. Finally, there is scant information about which biodiversity components are key to religious and spiritual values.

**Selected examples on the links between biodiversity and ecosystem services**

**Forage**

Grasslands provide forage for livestock, from which we gain meat and milk products. There is considerable evidence that more aboveground plant biomass can be produced by diverse than by depauperate grassland plant communities. It remains unclear, however, whether this will necessarily lead to greater production of meat and milk products. Early trials on forage diversity were inadequately designed to test for plant diversity effects on forage production. Furthermore, most modern grassland biodiversity experiments have not included livestock grazing; focused on species commonly used as forage; considered the impacts of changes in plant diversity on the quality of forage, including its nutritional value (crude protein content) and digestibility (lignin and cellulose content); or considered the health and growth of livestock.

A few recent studies have begun to address these limitations (e.g., Isbell and Wisley, 2011). Results show that increasing plant diversity can: i) increase biomass production under intense livestock grazing; ii) increase biomass production for common forage species; iii) increase biomass production without decreasing nutritional value or digestibility; iv) decrease the risk of mineral deficiencies or toxicities for beef cattle; and v) increase the biomass and nutrient intake by sheep. Given that managed grazing is the most extensive land use worldwide, there may be considerable value in conserving or restoring plant diversity in grasslands worldwide.

**Marine fisheries**

Fisheries provide a critically important source of protein, income, and jobs. Fisheries services are produced by complex interactions between environmental conditions, management, and biology. The contribution of diversity to fisheries is not yet well-resolved. The quality and quantity of evidence varies with scale and the component of diversity considered.

Theory and examples from other ecosystems suggest that biodiversity could increase or stabilize long-term yields or enhance their resistance and resilience to environmental fluctuations. Yet limited evidence is available to support these theories for fisheries, especially for resistance and resilience. On one hand, there is strong evidence that within species population diversity reduces variability in annual yields and fisheries closures for Alaskan sockeye salmon (*Oncorhynchus nerka*) via a portfolio effect (Schindler *et al*., 2010). In contrast, future studies are needed to explore the contributions of other forms of diversity, including functional diversity, functional composition, and relative abundance of different species.

The relationship between multiple-species marine fisheries and other forms of diversity remains muddled. At a global scale, Worm *et al*., (2006) suggest that diversifying targeted species can increase fisheries’ productivity and stability while decreasing their probability of collapse. This study, however, did not control for other factors known to influence fisheries yields: environmental factors (e.g., primary productivity) and management. Others suggest that primary
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productivity – rather than species richness of ecosystem – drives fisheries production (Chassot et al., 2010) or that this effect is instead driven by body size (Fisher et al., 2010). One reason for these inconsistencies may be that these relationships were explored using broad-scale correlations at a global scale. Testing more mechanistic hypotheses about why and how different forms of biodiversity could influence fisheries could progress our understanding of the pathways through which biodiversity affects fisheries.

Soil fertility

Soil fertility can be defined as the physical, chemical, and biological condition of the soil required for plant growth and development that is inherently linked to the capacity to produce biomass in natural and agricultural ecosystems (Barrios, 2007). Complex feedbacks between plant and soil biodiversity play fundamental roles in ecosystem functions related to soil fertility generation and renewal. The soil biota contributing to soil fertility is extremely diverse, ranging from invisible microorganisms to macro-fauna such as earthworms and termites. However, the soil biodiversity–ecosystem service relationship appears to be less related to species richness and more dependent on certain key species or species with particular traits. Based on their contribution to aggregate ecosystem functions underpinning soil-based ecosystem services, soil organisms can be grouped into four keystone functional assemblages (Kibblewhite et al., 2008): i) decomposers; ii) nutrient transformers; iii) ecosystem engineers; and iv) bio-controllers.

While soil organisms are largely not visible, this ‘hidden’ biodiversity contributes to soil fertility in many ways (Barrios, 2007). They are the principal driving agents of nutrient cycling. They regulate the dynamics of soil organic matter formation and breakdown which directly impacts soil carbon storage and greenhouse gas emissions. They modify the physical structure of soil through their effect on the aggregation of soil particles, which directly affects water regimes. They enhance the amount and efficiency of nutrient acquisition by crops and native vegetation through symbiosis with mycorrhizal fungi and nitrogen-fixing bacteria. Further, they influence plant health through the biological control of pests and diseases by their competitors, natural predators and parasites. Until recently, linkages between soil biodiversity and ecosystem services received little attention. It is now increasingly evident that soil biodiversity is critical for a sustainable human existence.

Water quality

Water quality is often determined by levels of chemical (e.g., nitrates), microbiological (e.g., fecal bacteria), or physical (e.g., soil particles) pollutants. The amount of pollutants that is acceptable varies among different types of uses (e.g., irrigation vs. drinking water) and among contexts (e.g., different countries). The avoidance, removal, and storage of these pollutants are key ecosystem services.

The chemical, microbiological, and physical quality of water at the point of human use can depend on many factors. For example, chemical pollutants can be regulated by river organisms through the processing of nutrients or toxic substances during metabolic breakdown. Transiting chemical pollutants are exported through the food web, and can find their way either downstream or to the top of the food chain. Microbiological quality is often linked to catchment management (Wilkes et al., 2013). Finally, river physical quality, for example temperature or flow, is often dependent on the character of riparian vegetation.
However, we lack field evidence on how much waste can be processed by river biota before the maintenance of biodiversity, its ability to regulate water quality, or fish production are impaired. There is a clear need to quantify in situ regulation services provided by river biota for water quality and to identify resilience thresholds, in particular under different land use and climate scenarios. As pressure on quality water rises, water companies and governments are likely to increasingly look to these natural solutions to provide cheaper and more sustainable water provision.

**Regulation of human disease vectors**

Biodiversity is important in contributing to ecosystem services that promote livelihoods and well-being. But in some cases, biodiversity itself is much more closely linked to human health, and not necessarily in a positive way. Biodiversity represents a disease threat to humans in many circumstances. For example, many wildlife species act as hosts of disease that can have significant negative economic and well-being impacts on humans (Daszak et al., 2000). Wildlife has been the origin of many emerging infectious diseases in recent years.

However, biodiversity may also have benefits to human health through protecting against or reducing disease, through a ‘dilution effect’. Disease risk decreases as the diversity of an animal community of potential hosts increases and thus the relative abundance of the key host for that disease decreases. Such a dilution effect is enhanced where hosts vary in their quality for pathogens or vectors, and where an abundance of low-quality hosts or vectors reduce the encounter rates of high-quality hosts with pathogens and vectors (Ostfeld and Keesing, 2012). Empirical evidence for this link between species richness and disease regulation is limited but growing.

Moreover, empirical evidence shows that, more often than not, biodiversity loss actually increases disease transmission (Ostfeld and Keesing, 2012). In a review of the statistical relationships between biodiversity and disease transmission, it was found that 80% showed a significant negative association (dilution effect), whereas only 12% showed a significant positive association (amplification effect) (Cardinale et al., 2012).

**Existence value of species diversity**

The existence value of species diversity arises from the satisfaction people derive from the knowledge that a species exists. This value is ultimately emotional and derived from feelings and preferences about non-human living species. The existence value of species is thus mediated by two main factors: i) people’s affective and emotional responses to species; and ii) people’s self-interest related to the utility derived from species. This dichotomy has been referred to as anthropomorphism vs. anthropocentric, affection vs. economic self-interest, empathy/identification vs. instrumental self-interest, affect vs. utility.

One of the most common indicators to measure the existence value of species is the willingness to pay. Specific morphological traits (e.g., size, round forms or eyes sizes) and the phylogenetic closeness of the species to humans both contribute to the existence value of species, besides various socioeconomic factors. Mammals, birds, and species with neotenic characteristics are among the most widely preferred.

Measuring the existence value of species in contexts where people cannot meet their most basic needs and where the conservation or enhancement of biodiversity may necessitate a
trade-off with livelihoods or food is much more challenging on both methodological and ethical grounds.

**Linking biodiversity, ecosystem services and the different components of well-being**

Ecosystem services are a social construct, and they only exist where humans gain some degree of well-being from their interactions with ecosystems. Human well-being is a multifaceted concept which includes the presence of positive emotions and moods (e.g., contentment, happiness), the absence of negative emotions (e.g., depression, anxiety), satisfaction with life, fulfilment, resilience and positive functioning (Centers for Disease Control and Prevention, no date).

Wellbeing components depend differentially on financial, social, infrastructure and natural capital. Adequate nourishment, access to clean drinking water, or access to traditional medicine are examples of needs that depend largely on ecosystem services. Plant species richness can contribute to higher forage production, sufficient meat production, and meeting basic food security needs (Figure 4.1). Fish population diversity can contribute to yield stability and thus food and job security (Schindler et al., 2010). Appreciated plants and animals can contribute to aesthetic enjoyment, spiritual and mental health and thus to overall health and good social relations. Yet the relative contribution of biodiversity itself to these different components of wellbeing is much harder to assess (Landers et al., 2016).

**Figure 4.1** Biodiversity is linked to ecosystem services and the different components of wellbeing. Selected examples are used to illustrate these linkages.

*Source:* modified from MA, 2005 and Mace et al., 2012
Complex interlinkages between biodiversity and services: resilience, trade-offs, scaling, substitutability, and sustainability

Global change brought by increasing population needs and altered climatic patterns is expected to affect biodiversity, ecosystems, and ecosystem services, with significant impacts on social and economic well-being. But despite mounting concern about the severity of these issues, knowledge about the complex interlinkages between biodiversity and services, involving multiple scales, non-linear dynamics, and trade-offs, is limited and disconnected.

Ecosystem services are ultimately supplied by the interactions between societies and ecosystems through social-ecological systems. Thus, the resilience of service supply will depend not only on biodiversity but rather on the whole set of biophysical and societal variables that underpin services provision. For instance, soil fertility maintenance will depend on the functional resilience of the different components of soil biodiversity contributing to the physical, chemical, and biological soil attributes that sustain land productivity (Barrios, 2007). Yet soil fertility is also influenced by soil type (e.g., parent material, texture, type of clay) and soil management: the types of crops (e.g., annuals vs. perennials), land cover (e.g., dense vs. sparse stands), diversification (e.g., monocropping vs. intercropping), management practices (e.g., tillage vs. no-tillage), and the utilization of inputs (e.g., fertilizers, irrigation).

Bundles of services rather than individual ones result from a particular configuration of biophysical, management, and societal drivers. Biodiversity may have positive effects on some services but negative or no effects on others. Agroecosystems can be managed to maximize yields or to maximize yield security through the regulation of agricultural pests and diseases, or to maintain soil fertility through time. They can also be directly or indirectly managed to maximize water infiltration in soil or soil carbon stocks. Thus assessing the contribution of plant and soil biodiversity to the services from agroecosystems and their resilience will depend on understanding how the changes to biodiversity affect individual services, as well as synergies and trade-offs among services (Balvanera et al., 2014).

At larger spatial scales, maintaining habitat heterogeneity and connectivity in landscapes and seascapes allows for the maintenance of biodiversity while at the same time allowing for the supply of a larger portfolio of ecosystem services. Such heterogeneity is likely to contribute to that of key provisioning and regulating services. For example, designing marine reserve networks can simultaneously enhance conservation of biodiversity, reduce fishery costs, and even increase fishery yields and profit.

Much work is still needed. For instance, we need to explore whether species can easily be substituted and still provide an equivalent ecosystem service, although it has been shown that this is unlikely if we are interested in multiple services at large spatiotemporal scales in a changing world (Isbell et al., 2011). Also, we need to assess how sustaining biodiversity meets the needs of multiple stakeholders that differentially benefit from services and trade-offs.

Also, changes in human well-being mediated by biodiversity and its interactions on ecosystem services will in turn influence decisions on biodiversity and ecosystem management. While a subject of debate, demonstrating the role of biodiversity may be beneficial for biodiversity conservation, although some species risk being at a disadvantage if their ‘service record’ cannot be proven. Alternatively, ecosystem services should be one of several factors considered in such decisions. However, one of the biggest remaining challenges is understanding and predicting how the perceived values of services will have feedbacks on biodiversity and ecosystems.

Increased understanding of the role of biodiversity on sustaining ecosystem services is likely to increase the relative value of services that are still currently taken for granted, such as water
quality regulation. This is particularly true in the context of short-term local decision-making in which declines in ecosystem services are not apparent and thus not taken into account.

New perspectives for addressing the links between biodiversity and ecosystem services at different spatial scales

Local and landscape scale research can provide new insights if designed with a global vision to contribute to current global challenges of the Convention on Biological Diversity (i.e., Aichi targets) as well as the newly constituted Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). We need to understand how and when the links between biodiversity and ecosystem services are dependent on the biophysical, management, and societal context. Integrated interdisciplinary research is needed to understand the consequences of different types of management for the key components of biodiversity that underpin different bundles of ecosystem services and for the benefits derived by stakeholders (Nagendra et al., 2013).

A new network of long-term, interdisciplinary, adaptive, and participatory studies can be used to fully assess the contributions of biodiversity to ecosystem services and people’s well-being (Figure 4.2). For instance, a network of sites with contrasting social and ecological conditions and a common experimental design could be used to monitor biodiversity, different bundles of services and the flow of benefits to societies (Balvanera et al., 2014). Designing and monitoring management experiments with stakeholders would ensure that the experiments/monitored variables were the most relevant to society. With this design, the marginal

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**Figure 4.2** Steps leading to a new generation of biodiversity and ecosystem services research, using the effects of biodiversity through soil functions on long-term crop yields as an example.

*Sourced from Balvanera et al., 2014*
contribution of biodiversity to not only ecosystem services but also the satisfaction of stakeholder's needs could be assessed.

Studies focused on biodiversity management across gradients of intensification in tropical agricultural landscapes, currently under greatest threat of biodiversity loss, would constitute a useful starting point (Jackson et al., 2012). Emphasis on agricultural practices that embrace ecological intensification through relatively high, but manageable, levels of aboveground and belowground biodiversity (e.g., agroforestry) would be key to addressing fundamental questions on the role of plant-soil feedbacks in the provision of ecosystem services required for sustainable agriculture. The strong linkage between plant functional traits and soil biodiversity highlights the potential to strategically utilize agricultural management systems to influence the provision of soil-mediated ecosystem services in agricultural landscapes. Furthermore, integrating local and technical spatial variability information on ‘hot spots’ of soil biological activity and focusing on functions that are relatively specific, such as the roles of ecosystem engineers or specific nutrient transformations, would help to achieve more reliable assessments of the links between biodiversity and ecosystem services (Barrios, 2007). The focused approach mentioned earlier, however, should be embedded in an interdisciplinary framework where land use decisions and the provision of ecosystem services represent the outcome of the continuous interaction between functional diversity components and the priorities of social actors.

A multi-scale approach would also be needed, given that ecosystem services are supplied, used, and managed at different spatial scales. The interlinkages between biodiversity and ecosystem services could then be assessed at different scales, ranging from local to landscape, regional, and global scales. Observations and experiments could be combined with the analysis of models for biodiversity, ecosystem services, and impacts on human well-being at different spatial scales.

Such multi-scale assessments need to be undertaken by large interdisciplinary teams of researchers and other relevant stakeholders. The good news is that such networks are currently under construction and in some cases already in place. For example, the BESS (see http://www.nerc-bess.net) programme funded by the UK Research Councils is already bringing more than 120 researchers and 50 stakeholder organizations together to investigate the role of biodiversity in sustaining ecosystem services across all UK landscapes. At a more global scale, Future Earth (www.icsu.org/future-earth), the new encompassing global environmental program and its associated projects (e.g., on Ecosystem Change and Society, www.pecs-science.org), is exploring ways to tackle some of the questions posed above. Research and communications networks such as the Ecosystem Services Partnership (www.es-partnership.org) provide opportunities to form a network of researchers and stakeholders across ecosystems and regions, and to respond to some of the pending issues. Overall, such communities can inform decision-makers at different spatial scales and across countries and to contribute to the endeavour faced by IPBES.

Conclusions

Biodiversity is closely linked to most ecosystem services but generally not in a simple way. The nature of the relationship between biodiversity and ecosystem service delivery still remains unknown for most ecosystem services. For those that are known, relationships are highly variable and may be positive, negative, or non-linear (Table 4.1). The number, identity, functional characteristics, and evenness of species are important to ecosystem functioning and consequently to the supply of different types of services. Useful concepts and approaches, such as
Biodiversity and ecosystem services

Table 4.1 Summary of different general types of known relationships between biodiversity (BD) and ecosystem services (ES).

<table>
<thead>
<tr>
<th>Type of BD-ES relationship</th>
<th>Impact of BD loss on ES</th>
<th>Basis for relationship</th>
<th>Types of services</th>
<th>Relevant examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Positive</td>
<td>Negative</td>
<td>Theory – complementarity effect, selection effect, insurance hypothesis</td>
<td>Provisioning</td>
<td>Biomass production for forage for livestock (Finn et al., 2013)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Empirical – fisheries</td>
<td></td>
<td>Within-species population diversity reduces variability of annual fisheries yields (Schindler et al., 2010)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Globally, greater species richness of targeted species can increase fisheries productivity and stability (Worm et al., 2006)</td>
</tr>
<tr>
<td>Negative</td>
<td>Positive</td>
<td>Empirical evidence</td>
<td>Provisioning</td>
<td>Some highly intensive horticulture and crop production, where much biodiversity perceived as pests</td>
</tr>
<tr>
<td>Flat</td>
<td>None</td>
<td>Empirical evidence</td>
<td>Cultural</td>
<td>Landscape-based recreation which is not biodiversity-dependent (Quijas et al., 2012)</td>
</tr>
<tr>
<td>Hump-shaped</td>
<td>Variable</td>
<td>Empirical evidence</td>
<td>Cultural</td>
<td>Landscape aesthetics – preference for extensively managed landscapes over intensively managed or unmanaged ones (García-Llorente et al., 2012)</td>
</tr>
<tr>
<td>Non-linear or variable</td>
<td>Variable – determined by species composition and functional traits rather than biodiversity per se</td>
<td>Empirical evidence</td>
<td>Provisioning</td>
<td>Harvesting of individual species from extensive or non-managed systems (Chassot et al, 2010)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Theory – amplification and dilution effects for disease</td>
<td>Regulating</td>
<td>Regulation of soil fertility in many ways (Barrios, 2007, Kibblewhite et al., 2008)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Regulation of infectious disease (Ostfeld and Keesing, 2012)</td>
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<td></td>
<td></td>
<td></td>
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<td>Regulation of pests and invasive species (Wilsey and Polley, 2002)</td>
</tr>
</tbody>
</table>

ecosystem service providers and trait-based approaches, and an understanding of the mechanisms through which diversity regulates ecosystem function, have advanced our understanding of these interlinkages.

Alas, the large variety of services, the multiple scales at which they operate, and the multiple ways in which different processes and types of services link to biodiversity hinder our integrated
understanding of entire systems dynamics. Evidence for most services and contexts is still in construction, largely due to lack of adequate documentation and testing, even for well-known examples such as forage, fisheries, soil fertility, water quality, and the regulation of human disease vectors.

Biodiversity likely influences the long-term maintenance of functioning social-ecological systems and the flow of benefits from nature to societies at multiple spatial scales. To understand these longer and larger-scale dynamics, multi-scale, interdisciplinary research in collaboration with stakeholders is needed. Long-term research and the assessment of multiple ecosystem services emphasize that losing a few species can be detrimental to service supply and thus human well-being. Improving our understanding of the consequences of biodiversity change can inform the design of new management interventions and policies, via platforms on Biodiversity and Ecosystem Services such as IPBES (www.ipbes.net), Future Earth’s ecoSERVICES (www.futureearth.org/projects/ecoservices) and the Ecosystem Services Partnership (www.es-partnership.org).

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References


Biodiversity and ecosystem services


Briefing Note 4.1  Service providing units

Gary Luck

In 2003, Gretchen Daily, Paul Ehrlich and I (Luck et al., 2003) introduced the concept of service providing units (SPUs) to underscore the importance of maintaining population diversity for the sake of species conservation and the provision of ecosystem services. Changes in populations can have major impacts on ecosystems independent of any changes in species diversity. We also aimed to promote SPUs as a heuristic tool to focus attention on the key components of species populations that would impact the population’s capacity to contribute to ecosystem service provision.

At the time, research on the services provided by plants and animals was in its infancy and centred mostly on identifying which species may or may not be contributing to service provision. We argued that a more complete understanding was needed, one which recognised that the number of species populations (population richness), the size and density of each population, the distribution of populations and their genetic differentiation were all vital to the level of contribution a species may make to a given ecosystem service in a particular location.

The SPU concept was introduced as a new approach to link a species population explicitly with the services that it provided. Moreover, the concept can be used as another way to delineate population boundaries, similar to related concepts such as evolutionary or demographic units (see Luck et al., 2003). For example, a population of native pollinating bees confined to an isolated patch of remnant rainforest may provide pollination services to an adjacent coffee crop, but not to other, more distant crops. This population may be nested within a single evolutionary unit or even demographic unit, but for the sake of the population’s contribution to ecosystem service provision it should be considered a discrete SPU and managed as such.

Various examples of SPUs now exist in the literature, even if not recognised as such by the authors themselves. Critically, these researchers have attempted to quantify at least one of the key population characteristics that are vital for understanding how a population may contribute to service provision. For example, Mols and Visser (2007) demonstrated the capacity of Parus major – an insectivorous bird species – to provide a pest control service in apple orchards by substantially reducing caterpillar damage to the crop. The authors showed that at a density of 1–6 breeding pairs per 2 ha, caterpillar damage is reduced by up to 50% compared to control sites with no breeding pairs. The SPU in this example is the density of breeding pairs within the orchard needed to deliver the service at the required level. At least one breeding pair of Parus major every 2 ha within the apple orchard would be a bare minimum. Another example of an SPU comes from Hougner et al. (2006), who demonstrated that the maintenance of oak forest in the National Urban Park of Stockholm required a minimum of 12 resident Eurasian jay (Garrulus glandarius – a major dispersal agent of oaks) pairs present each year for 14 years.

At a broader level, Schindler et al. (2010) provide a wonderful example of the importance of managing populations as discrete units in the context of ecosystem-service provision. In Bristol Bay, Alaska, sockeye salmon (Oncorhynchus nerka) exist in hundreds of locally adapted populations distributed among tributaries and lakes. These populations are reproductively isolated, have capacity for micro-evolution and are collectively adapted to a wide range of conditions. This population diversity and asynchronous dynamics leads to less variability in returns to the fishing industry that relies on this species. Schindler et al. (2010) estimated that variability in returns is over two times lower than it would be if the species existed in a single homogeneous population, and that closures
of fisheries would be ten times more common if the current diversity was reduced to a single homogeneous population.

The notion of quantifying the ecological units that provide ecosystem services applies beyond simply species populations and can include multi-species functional groups, entire ecological communities, habitat types or landscapes. In Luck et al. (2009), we united the concepts of SPUs and ecosystem service providers to demonstrate how different organisational levels can contribute to services in different ways. For example, maintaining the functional diversity of native pollinating bees can be crucial to delivering pollination services to watermelon crops in California (Kremen et al., 2004).

There is much to do to further understanding of the demographic, functional and genetic traits required to provide a particular service at a particular level in any given context. Quantifying these traits raises many challenges, but these must be tackled head on so that society is well informed about what needs to be protected to maintain the provision of vital services into the future.

References


