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10 Years Later: Revisiting Priorities for Science and Society a Decade after the Millennium Ecosystem Assessment

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SUMMARY

The study of ecological services is fast becoming a cornerstone of mainstream ecology, largely because they provide a useful means of linking functioning to societal benefits in complex systems by connecting different organizational levels. In order to identify the main challenges facing current and future ecosystem service research, we analysed the effects of the publication of the Millennium Ecosystem Assessment (MEA, 2005) on different disciplines. Within a set of topics framed around concepts embedded within the MEA, each co-author identified 5 key research challenges and, where feasible, suggested possible solutions. Concepts included those related to specific service types (i.e., provisioning, supporting, regulating, cultural, aesthetic services) as well as more synthetic issues spanning the natural and social sciences, which often linked a wide range of disciplines, as was the case for the application of network theory. By merging similar responses, and removing some of the narrower suggestions from our sample pool, we distilled the key challenges into a smaller subset. We review some of the historical context to the MEA and identify some of the broader scientific and philosophical issues that still permeate discourse in this field. Finally, we consider where the greatest advances are most likely to be made in the next decade and beyond.

Accepted version

Table of Contents

1. Introduction

2. Impact of the Millennium Ecosystem Assessment

3. Functional attributes and networks as frames for ecosystems and societies

4. Network approaches to ESs as a means of implementing the Millennium Ecosystem Assessment

5. Research priorities one decade after the Millennium Ecosystem Assessment

5.1. Underpinning knowledge - from functioning to services

5.2. Regulating services

5.3. Provisioning services

5.4. Supporting services

5.5. Cultural and aesthetic services

5.6. Synergies among services and multiple drivers - how can we quantify main effects and interactions among ESs and their drivers in the real world?

5.7. How are services linked in different realms?

5.8. How do we prioritize the "value" of services?

5.9. Coupling models to data - how do we develop a better predictive understanding?

5.10. How can we manage systems for sustainable delivery of ESs?

5.11. What is the role of global connections in ESs delivery, and how should this impact our management and understanding/prediction of future provision?

6. Preliminary conclusions

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References

1. Introduction

The concept of Ecosystem Service (ES) is increasingly coming to the fore across a range of disciplines that span both the natural and social sciences (e.g., Díaz et al., 2006; Carpenter et al., 2009; Naidoo et al., 2010; Naeem et al., 2012; Bohan et al., 2013; Bennett et al., 2015; Gill et al., 2015; Pocock et al., 2015; Vacher et al., 2015). Although many of the underlying tenets are not necessarily novel *per se* and analogous phenomena have been described in various guises over several decades, a unified language has emerged only relatively recently, following the rise of a suite of multidisciplinary approaches. Much of the current predominance of ESs can be traced back to the crystallisation of these ideas in the Millennium Ecosystem Assessment, published a decade ago (MEA, 2005). With the benefit of hindsight, it is clear now that this was a seminal moment in ecological research, assembling a large international community for work that produced repercussions for policy and research during the following decade. It is timely to reflect on the major advances made during these years and to identify the future challenges. Rather than a comprehensive coverage of what is now a vast and varied field of research that is becoming a recognisable discipline in its own right, this paper presents a collation and distillation of the views of a sample of experts, some of whom helped shape the thinking behind the MEA, and others who represent the new generation of researchers who have emerged within the increasingly multidisciplinary world forged by the MEA. In particular we sought to explore how new frameworks might be adopted to advance the field, with an emphasis on the potential of network-based approaches, given that we are dealing with complex systems comprised of many interacting parts.

Since the publication of the MEA, a considerable amount of research has centred on strengthening its conceptual framework by providing theoretical and empirical tests of core ideas. Often, the objective of this research was to enable two activities: monetary valuation of ESs and linking ESs to socio-economic systems. Part of that process has inevitably led to a search for indicators of the status of ES and whether human interventions have negative or positive consequences. Many environmental factors that could potentially affect ESs are now being measured to gauge their utility as predictors and indicators of change, some of which are relatively closely linked to biodiversity or ecosystem functioning (e.g., fish production), whereas others are more abstract and challenging to measure rigorously (e.g., cultural significance of riverine bird species), although scenario-building approaches and new visualisation tools are helping to bridge these gaps (Sutherland et al., 2013; Pocock et al., 2015). In some cases, a range of indicators of ESs change are currently being employed in management practices associated with ES delivery (cf. Liss et al., 2013). These approaches are still relatively narrow in scope, with the number and type of services restricted to the few that are easiest to measure (Perrings et al., 2011; Daw et al., 2015). This scope needs to be broadened if ES indicators are to be widely applicable, but to do so is difficult given the enormous range of ESs and the many variables that determine their magnitude, dynamics, interactions and trade-offs at all levels, including whom the beneficiaries are.

Complex (living and non-living) systems comprise relationships among their components, and the number, pattern, and dynamics of such relationships being regarded as measures of system behaviour (Mesarovic, 1984). Complex system theory could provide a valuable means for developing a more comprehensive and integrated understanding of ES dynamics, as it deals explicitly with the mix of direct and indirect actors and consequences that are a defining characteristic of ES research. Can the behaviour of a system capture the value of ESs? According to Holling (1987) and Gunderson and Holling (2002), the behaviour of a living system results from an interaction among four basic functions: (1) exploitation (e.g., via rapid

colonisation), (2) conservation (e.g., resource accumulation), (3) release (stored resources suddenly released after external disturbances) and (4) reorganization (making the released resources easily accessible for a novel colonisation). Holling's classification can be applied to both living and non-living systems (Costanza et al., 1997; Walker and Salt, 2006) and can be adapted to help integrate ecological economics and ESs in a more coherent manner than is currently the case.

General concepts of ESs have been in use for more than three decades (Ehrlich and Mooney, 1983), reflecting longstanding and widespread concerns that global changes have potentially strongly and adversely influenced terrestrial and aquatic communities. The MEA, which grew out of these earlier ideas, is arguably the most successful and enduring framing of scientific questions concerning biodiversity, ecosystem functions, ecosystem services and human wellbeing in complex socio-ecological systems. It was established to help develop the knowledge base for improved decision-makings in recognition that *"it is impossible to devise effective environmental policy unless it is based on sound scientific information"* (Millennium Report to the United Nations General Assembly, 2000). This text continues *"While major advances in data collection have been made in many areas, large gaps in our knowledge remain in how to use the MEA framework for this ever increasing wealth of data on environmental factors and human activities. In particular, there has never been a comprehensive global assessment of the world's major ecosystems."* The MEA viewed ecosystems through the complex science-policy lens of society, how ESs provide benefits to people, and how human actions alter ecosystems and the ESs they provide to humanity (Carpenter et al., 2009). Among multiple science-policy frameworks, the ES concept is undoubtedly now by far the most popular (Figure 1).

<FIGURE 1>

Concepts like ESs, which integrate natural and social factors that link ecosystems with human societies, have triggered new waves of scientific research. Any consideration of ESs should centre on linking ecological, socio-economic and related disciplines and will benefit from the approaches and insights gleaned from MEA, with its broad frameworks that linked nature (i.e., biodiversity and ecosystem functions) with ecosystem services and human wellbeing (Figure 1), although some papers have attempted to deal with the difficulties of connecting ESs to human wellbeing (Fischer et al., 2008; Carpenter et al., 2009). These and similar works clarified the need to separate benefits to people from ecosystem functions (Fischer et al., 2008; Fischer and Turner, 2008). However, governmental bodies have *de facto* a long history of bridging the gap between human wellbeing and ecosystem functioning.

For a long time environmental policy in Europe was predominantly concerned with pollution remediation of soil, water and air. In the United States, the Wilderness Act was passed in 1960s and all the major US legislations for endangered species, air pollution and toxicity were passed in the 1970s (even the Clean Water Act, enacted in 1948, was completely rewritten in 1972 and 1977). Since the 1970s, environmental legislation has broadened its remit and coverage of the major ecosystems, with a general progression from a focus on the immediate vicinity of human populations on land to more distant ecosystems, including the remote ocean depths. Worldwide, there are many historical examples of how freshwaters have been used and modified by humans for millennia (Palomo et al., 2015), although water pollution management came much later due to lack of appropriate monitoring tools (e.g., Friberg et al., 2011). When the first cases of soil pollution became apparent remediation was regarded as a minor operation that could be carried out by national governments, in contrast to

transboundary air pollution, which demanded international cooperation, as in the classic case of identifying the causes and ecological consequences of nitrogen deposition and acid rain (Sala et al., 2000; Friberg et al., 2011; De Vries et al., 2015). International problems provided an impulse for international policy, at the same time that scientific cooperation and coordination of efforts were strengthened by disasters like Chernobyl. Within this globally changing environmental and legislative landscape, the MEA framework has become increasingly central to understanding how to couple ecological and social systems across many scales and how to evaluate the effects of resource degradation and mismanagement. Maintaining, enhancing, and, if necessary, restoring ESs has now become a high-level policy goal, leading to many large-scale projects, such as the drive to restore many river catchments across much of Europe (Feld et al., 2011), where the true societal and economic cost of centuries of pollution and habitat destruction are now recognised.

Unprecedented efforts have been made to document, analyse, and understand the effects of environmental change on ecosystems and human wellbeing, and to cast those effects as ESs within a cross-disciplinary conceptual framework that integrates environmental, social, and economic theory (Figure 1). The first group of studies concentrates on local scales, identifying the relationships and connections between the diverse spectrum of ecological processes provided by ecosystems and social factors related to the core constituents of human wellbeing. The second group situates services and wellbeing within a direct and indirect context of drivers of environmental change (e.g., nitrogen deposition, elevated CO₂, biodiversity loss). These entities are primarily operational at a larger, even global scale, with deforestation and desertification being two classic examples of worldwide ES disruption (Ehrlich and Mooney, 1983). Daw et al. (2011) and Poppy et al. (2014) highlighted the need to understand the dimensional aggregation of these component groups, asking who benefits from different ESs and who takes decisions about different ESs. Such a (dis)aggregation requires effective visualisation tools, like networks, and here we suggest possibilities to achieve this goal.

2. Impact of the Millennium Ecosystem Assessment

Human health is (on average across the globe) better today than ever before, and, together with unprecedented population growth due to public sanitation improvements, health and wealth are arguably the main underlying factors behind the huge environmental impacts we see in almost all ecosystems (Whitmee et al., 2015). If we are to maintain and improve the wellbeing of the ever-increasing human population, we need to understand and manage the consequences of this growth for the natural ecosystems we interact with, both directly and indirectly. Stress ecology, social ecology and sustainability science have received growing attention, especially in the light of projections that the global population could reach ten billion by 2050, associated with sustained large-scale migrations from rural to urban areas.

To gain an overview of what, if anything, has changed noticeably within the relevant environmental sciences during the last two decades, following the MEA's publication, we conducted a literature search from 1995 to 2015 using Thomson-Reuters's ISI on the Web of Science core collection with a range of broad primary search terms (NUTRIENT CYCLING or SOIL FORMATION or PRIMARY PRODUCTION) as well as a suite of more specialized secondary terms ([FOOD or FRESH WATER or WOOD AND FIBER or FUEL or CLIMATE REGULATION or FLOOD REGULATION or DISEASE REGULATION or WATER PURIFICATION or AESTHETIC or SPIRITUAL or EDUCATIONAL or

RECREATIONAL] and ["ECOS* SERVICE*" or "ECOL* SERVICE *"]). Together these searches returned a total of 22,532 peer-reviewed articles, mostly from the subject areas: 'ENVIRONMENTAL SCIENCES ECOLOGY', 'MARINE FRESHWATER BIOLOGY', 'OCEANOGRAPHY', 'GEOLOGY', 'AGRICULTURE', 'FORESTRY', 'PLANT SCIENCES', 'BIODIVERSITY CONSERVATION', and 'METEOROLOGY ATMOSPHERIC SCIENCES'. An additional search conducted on (BIODIVERSITY and ["ECOS* SERVICE*" or "ECOL* SERVICE *"]) returned 4,111 peer-reviewed papers from 1995 to 2015 (mostly from the subject areas: 'ENVIRONMENTAL SCIENCES ECOLOGY', 'BIODIVERSITY CONSERVATION', and 'AGRICULTURE') that were included in the final data set ($n = 26,643$).

Assessing the difference in the number of publications on ESs before and after MEA revealed an almost exponential growth, manifested principally as interdisciplinary links that developed between environmental scientists, ecotoxicologists and ecologists. This has resulted in a widespread adoption of ecological theory, much of which has been driven by the emergence of the ecosystem approach and a growing focus on provisioning of goods and sustainability (Figures 2 and 3). The MEA, which in its various forms has itself been cited in the peer-reviewed literature over 10,000 times, clearly contributed significantly to putting ES firmly on the agenda.

<FIGURE 2>

Building on early works by Costanza and Daly (1992), Perrings et al. (1992), and Daily (1997), the MEA recognized benefits that people receive from nature as goods and services. These include direct benefits (such as food); indirect benefits (such as regulating the climate); intangible benefits (such as a sense of wellbeing from knowing natural ecosystems exist); and future benefits (belief that we continue to have the option to benefit from goods and services into the future) (Bateman et al., 2011). By catalyzing the ES approach at a global scale, the MEA boosted societal and political awareness that protecting ecosystem functioning and maintaining balance between supplies and demands of goods and services are essential prerequisites for human wellbeing. An intriguing example of how societal values regulating ESs is given by the case of water purification: clean water has become a *conditio sine qua non* of civilisation since the ancient water and wastewater systems of Imperial Rome, but despite the huge knowledge accumulated in more than two millennia, it has been taken for granted in most societies. Its increasing shortage and the capacity of ecosystems to provide clean water have now turned it into a primary ES, in drylands and elsewhere (Figure 3).

<FIGURE 3>

In the decade since its publication, the MEA has contributed to putting anthropogenic disturbance firmly on the political and scientific agendas. We conducted additional Web of Science surveys from 1995 to 2015 with the following search terms: ("NITROGEN DEPOSITION" or "NITROGEN-DEPOSITION" or "N DEPOSITION" or "N-DEPOSITION"), ["LIGHT POLLUTION" and (BAT* or BIRD* or MOTH * or ECOL*)], ("LANDSCAPE FRAGMENTATION"), and [ECOL* and ("AGRICULTUR* INTENSIFICATION" or "RURAL INTENSIFICATION")], mostly from the subject areas: 'ENVIRONMENTAL SCIENCES ECOLOGY', 'PLANT SCIENCES', 'AGRICULTURE', 'GEOLOGY', 'METEOROLOGY ATMOSPHERIC SCIENCES', 'FORESTRY', and 'BIODIVERSITY CONSERVATION'. Human-driven effects of landscape and habitat fragmentation ($n = 1,137$, Figure 4) and light pollution ($n = 115$, Figure 5, upper panel)

exhibited a particularly rapid increase in publications, whereas global drivers like atmospheric deposition ($n = 4,679$, Figure 5, lower panel) maintained the rate of increase (flatter trend). ESs as a whole have proven to be robust and (relatively) straightforward for dealing with otherwise overwhelmingly complex socio-ecological systems, and to do so in an integrative way that has grown in popularity among scientists and decision-makers (Paetzold et al., 2010; De Groot et al., 2010; De Vries et al., 2015; Stoll et al., 2015). This view is reflected in various environmental legislation of the European Union, such as the Habitats Directive, the Water Framework Directive (EU, 2000) and the European Marine Strategy Framework Directive (EU, 2008, 2010).

<FIGURE 4>

<FIGURE 5>

3. Functional attributes and networks as frames for ecosystems and societies

At the macroscale, ecosystems and human societies possess comparable attributes, insofar as they contain multiple interacting entities, such as individuals, species or institutions, that respond both directly and indirectly to perturbations (Levin, 1998, 2000). Consider two instances: (1) any given ecosystem may incorporate continuous competition and facilitation among its species and functional groups, yet maintain ecological cohesion, and (2) any given society may incorporate continuous competition and facilitation among its members and social groups, yet maintain cultural and economic cohesion. Both instances share horizontal diversity between subsets of similar entities and vertical diversity at different (energetic, cultural, economic) levels and layers. Although the usage of these terms is consistent with that employed in MEA (2005), our interpretation of (functional) entities and (horizontal and vertical) diversity is now much broader and also incorporates other types of entities and diversities in general network theory. Understanding horizontal and vertical interrelationships among these entities is critical for management decisions, making appropriate tools necessary, especially as indirect responses to perturbations can be as strong as, or even stronger, than direct effects (Montoya et al., 2009; Moretti et al., 2013). Hence, tools to integrate such disparate repositories of knowledge and different forms of information are required; for instance by identifying novel opportunities, assessing threats or defining new issues (Sutherland et al., 2006, 2010, 2011). Importantly, natural ecosystems and human societies are not mutually exclusive, but are intimately connected – though they are still rarely studied with this perspective. As subsequently shown in this paper, they are interdependent and dynamically connected, so to understand and predict the behaviour of one system requires an understanding of the other.

Similarities between ecological and social disciplines are often hard to identify, even though ecological and socio-economic disciplines are historically linked in their formation, if not always in their academic study. In their simplest form, cities, landscapes and ecosystems are all open dissipative thermodynamic systems whose energy entrainment is (often assumed to be) maximized to confer stability against external disturbances (e.g., Heal and Dighton, 1986; Bettencourt et al., 2007; Kennedy et al., 2015). This leads to self-organising structures requiring close integration of those units needing efficient servicing (Bettencourt et al., 2007; Kennedy et al., 2015), a continuous process whose apparent complexity reflects simple universal scaling laws (Bettencourt et al., 2007; Um et al., 2009). In the case of ecosystems, Carpenter (2003) suggests avoiding the term equilibrium, as this implies exclusion of the

many other forms of steady-state dynamics seen in nature. Stability is not necessarily a static condition, whereas equilibrium is, but rather it is often a constrained or bounded dynamic process. Extremely low rates of change can resemble stability for many purposes, though not, technically, at equilibrium or even exhibiting stable dynamics (Holling, 1973).

Within this framework, even seemingly completely different data from ecological and socio-economic systems often appear to converge towards surprisingly similar phenomena. For instance, the frequency of sightings of bird species in the United States (e.g., a cultural or aesthetic ES) and the human population of cities (the ES recipients) in the United States share very plausible scaling laws (Clauset et al., 2009; but see also Stumpf and Porter, 2012, for caveats). Whether they are large cities, bird records or vegetation units, the huge amount of data available is useful for integration into ecological, social and economic networks, although terminology can be rather confusing as too often the same term has rather different meanings in different fields. For these, and many other reasons, modelling of complex socio-ecological systems remains a major challenge in contemporary trans-disciplinary research (Filatova et al., 2013). This task demands a comprehensive, interdisciplinary integration of ecological, social and economic aspects with well-developed conceptual frameworks and theoretical as well as simulation models (An, 2012) and thus, demonstrates the pressing need for high-quality data, as well as a shared lexicon of terms (Wallace, 2007).

Many stakeholders aim to achieve stable system conditions to remain within their “safe operating space”: such a sustainable system is presumed to be persistent in the mathematical sense, if protecting against extinction (species loss or collapse of societies) and maintaining the same set of options by avoiding critical collapses. However, if we visualize complexity in just two information layers, fragile behaviours seem to reflect a disorganized complexity in simple models but an irreducible complexity in complex models (Weaver, 1948; Alderson and Doyle, 2010). Recent efforts towards standardization are providing new ways by which multiple information layers can be mapped onto one another for evaluation and management of stocks and flows, or ESs (Madin et al., 2007; Raffaelli and White, 2013; Raffaelli et al., 2014). Investigating responses at different scales can therefore allow a much better integration of research, an integration based upon the most universal and oldest language of scientists, mathematics (Cohen, 2004).

It is possible to elucidate social ties in space, such as characterising how individuals (friends, relatives and contacts) use their cities, as any urban space comprises a physical infrastructure and a social network (Wang et al., 2015). In this context, the perspective of a spatial network can be used to visualise the dynamic conditions of sustainability in different systems by optimized, space-filling, hierarchical branching networks (Bettencourt et al., 2007). Similarly, networks are also widely used in the medical world to identify “disturbances” (e.g., Pichlmair et al., 2012). In the same way, it is possible to elucidate how entities in ecological networks are connected in space, for instance, how organisms (decomposers, producers, and consumers) separately break down, fix or derive their own energy, as any food web is comprised of a chemical backbone and a constrained space (Hines et al., 2015; Mancinelli and Mulder, 2015). Any network can thus be seen as a simple data structure, a graph whose nodes identify the elements of a system and whose links identify their interactions where most of the structural information of social and ecological networks seems comparable to each other (Figure 6). For instance, both the internet and the natural biosphere are promoted by an enormous variety of seemingly unrelated agents, and this could explain why both ecologists and social scientists have independently adopted network analysis as a common tool (Poulin,

2010): the challenge now is to use this common ground to help integrate these different disciplines more effectively.

<FIGURE 6>

4. Network approaches to ESs as a means of implementing the Millennium Ecosystem Assessment

The relationships between biodiversity, ecosystem functioning and services (B–EF–ES) have long been important gaps to address in ES studies across scales, but remain poorly understood despite many efforts (e.g., Luck et al., 2009; Mace et al., 2012). Originally, the focus was on quantitative biodiversity-driven relationships, founded upon estimations of species richness at different scales: a specific ecosystem or habitat, a regional area, or even a whole continent (Gotelli and Colwell, 2001; Hooper et al., 2005; Balvanera et al., 2006; Hector and Bagchi, 2007; Butchart et al., 2010; Magurran, 2013). Accordingly, ranking procedures (scores) were often used: at ecosystem level, scores are commonly calculated as the deviation from reference conditions (i.e., an expected species list in undisturbed systems), a methodology that can be easily visualized by path analysis or structural equation modeling (SEM). SEM enables causal understanding to be inferred more strongly from observational data (Eisenhauer et al., 2015; Hines et al., 2015), but is also highly sensitive to both the intrinsic quality of the data set and the quantity of the records. In addition, SEM requires the standard assumptions of linear modeling: multivariate normality, additivity, and linear responses (Mitchell, 1992; Shipley, 2002). These assumptions (often contrasting the shapes of the B–EF–ES curves), as well as the strengths and weaknesses of SEM and path analysis, are discussed in detail by Pugsek et al. (2003), Martínez-López et al. (2013) and Westland (2015). Therefore, network approaches may be more appropriate for the large and heterogeneous B–EF–ES data sets.

Many components of networks theory have evolved separately: most theoretical biologists and computer engineers focused on mathematical metrics of networks (Jonsson, 2014; Wang et al., 2015), whereas ecologists tended to focus on structural changes along environmental gradients (e.g., Mulder and Elser, 2009; Layer et al., 2010; Woodward et al., 2010). Systems biology raises the intriguing prospect that some networks are inherently easier to control than others (Liu et al., 2011), which could have clear implications for sustainable management of ESs, especially if generic traits or indicators of the system can be identified that reveal this tendency. From this perspective, many powerful tools are already applicable to elucidate the importance of the network's topology and a certain degree of universality arises as soon as characters of a network are sufficient to quantify its features, such as scaling exponents that capture allometric and hydrological laws (Dodds and Rothman, 2000).

Networks can help provide the necessary understanding of relationships among entities as metrics to evaluate the improvement of ESs. The form of a network can help both academics and non-academics visualize many functions of a given organism or group of species in an ecosystem (Pocock et al., 2015). For instance, shifts in detrital organic material supply can cause dramatic changes in community structure and ecosystem functioning (e.g., Ibanez et al., 2013; Mancinelli and Mulder, 2015) thus affecting the supply of goods and services. Furthermore, the many groups of species that exploit in a similar manner the same class of environmental resources can be visualized, indicating levels of redundancy and ecosystem resilience capacity: e.g., if one node (or species) is lost, there are many alternative pathways in the interaction network through which the effects of its loss are essentially short-circuited.

Also, developmental (successional) changes (Jonsson et al., 2005; Reiss et al., 2009), ecological stoichiometry (Mulder and Elser, 2009), overfishing (Jennings et al., 1999; Jennings and Blanchard, 2004), global warming (Yvon-Durocher et al., 2010), and fossil assemblages (Dunne et al., 2008) can be visualized by networks. Even at the level of individual variability in consumers' choice (Tur et al., 2014; Pettorelli et al., 2015), networks can be visualized and used to support conservation strategies based on resource requirements.

Ecological networks can be subdivided into three broad types: mutualistic plant–animal interactions, host–parasitoid and prey–predator (trophic) webs (Bascompte and Jordano, 2007; Ings et al., 2009). Their increasing popularity has led to many open-source software packages, such as 'Pajek' (Batagelj, 1998), 'bipartite' (Dormann et al., 2008), 'Gephi' (Bastian et al., 2009), 'Cheddar' (Hudson et al., 2013) and 'Food Web Designer' (Sint and Traugott, 2015) to visualize the different aspects of networks. These software packages also allow the extraction of mathematical descriptors related to ecological properties and services (e.g., biodiversity of interactions, the trophic basis of production) that can be used for comparative analysis and could ultimately form a suite of indicators for monitoring responses to anthropogenic stressors (e.g., food chains should shorten and networks should simplify as stressors increase).

From an empirical standpoint, the number and quality of agricultural network studies is rapidly improving: the rate of growth in this field is even faster than in more traditional ecology and, if it continues apace, network-based approaches in managed ecosystems are surely bound to shift from the sidelines into the mainstream (Bohan et al., 2013). The extension of metacommunity theory into metanetwork theory is now being pioneered in soil ecology and agroecology (Barberán et al., 2012; Pocock et al., 2012), largely due to the explicit recognition of the spatial and temporal patchiness of the landscape. This resonates with networks studies within the social sciences yet contrasts with much of traditional mainstream ecology, where spatiotemporal aspects are too often ignored as most studies are conducted in single, unreplicated systems, which are often (incorrectly) assumed to be isolated and closed systems.

The emerging field of eco-evolutionary dynamics is also being driven by studies of managed systems, in both fisheries science and agroecology, reflecting the extreme selective pressures being imposed by human activity and consequently the huge scope for ecological and evolutionary feedbacks to arise (Brennan et al., 2014). A good example of understanding feedback responses of human activities in managed systems is the use of pesticides: the rapid spread of pesticide resistance in commercial fisheries and the widespread alteration of freshwater community size-structures with attendant impacts on the food web are two pertinent examples that are attracting increasing attention. As pesticides cause regional biodiversity loss (Beketov et al., 2013) and erode different parts of the food web (Figure 7), networks can visualize in a detailed yet intuitive manner the consequences of the environmental impacts of pesticide run-offs on non-target organisms and their ES delivery (Text Box 1).

<FIGURE 7>

TEXT BOX 1 – SCIENCE FOR CITIZENS AND CITIZEN SCIENCE: TWO CASE STUDIES OF FRESHWATER ECOSYSTEMS

Since the maintenance of an ecosystem is largely tied to the beneficiaries of ES provision, in particular situations complex ecosystems are supposed to reduce human wellbeing (Lyytimäki and Sipilä, 2009). As an example, invasive zebra mussels in Lake Ontario and the St. Lawrence River in the USA were perceived to provide a positive contribution (benefit) by generating water clarity through filtration, as well as a negative contribution (disbenefit) by producing large amounts of nuisance algae (Limburg et al., 2015). The health risk associated with increasing water-associated pathogens (e.g., malaria) is another example where aquatic ecosystems are merely perceived to deliver a negative contribution to human wellbeing. These disadvantages (often defined as disservices, but see Section 6) are linked in human perception to disturbed aquatic systems, in which pathogen, pest, or parasite outbreaks are more likely to occur. To relate to the malaria example, in normally-functioning wetlands populations of regulating predators significantly reduce mosquito populations, thereby also diminishing associated health risks as increasing mosquito populations are usually linked to artificial aquatic systems, such as reservoirs. It is recognised that agricultural influence from heavily-fertilized agroecosystems causes substantial nitrogen leaching downward to the groundwater and laterally to the streams (Verhoeven et al., 2006; Gordon et al., 2010; Woodward et al., 2012). This increasing disturbance affects the functioning of wetlands and freshwater ecosystems, possibly leading to the disappearance of specialised species (e.g., Sterner and Elser, 2002). The hypothesis that healthy-functioning ecosystems overall deliver fewer disadvantages than disturbed ecosystems has yet to be tested. For instance, changes in land use and farming practices to feed rising populations have brought livestock animals increasingly close to rivers.

Citizen scientists, such as anglers, possess the skills to identify many macroinvertebrates and can monitor the status of ecosystems and report pollution incidents that threaten ES delivery. In the UK, biological tutors in conjunction with local agencies organise workshops to provide simple skills to citizen scientists whose data are valuable. Thompson et al. (2016) have recently shown how an insecticide spill in 2013 in the River Kennet altered the freshwater food-web structure and subsequently measured the resilience and recovery of the ecosystem across organisational levels from, the structure of entire ecological network and ecosystem functioning (embedded figure, right) to bacterial carbon substrate utilisation and molecular ecology (embedded figure, left). This provided a clear example of the close links between human society and natural ecosystems. The motivation for the Citizen Scientists to monitor the river's biota was a strong desire to ensure it was in a healthy condition.

*Embedded Figure Legend: Impacted sites D and F shown with dark (red) background and control sites A and C with a light (blue) background. Six months after the incident, the shrimp *Gammarus pulex*, which is a key component of the diet of the commercial fishes on the river and the main driver of leaf-litter decomposition rates, was the slowest taxon to recover. The pesticide spill had a wide range of direct and indirect repercussions for both the "brown" and "green" pathways in the food web, resulting in altered ecosystem functioning and service provision (e.g., suppressed decomposition rates but also undesirable algal blooms, and reduced prey availability as a supporting service for the commercial fisheries on the river). {FIGURE EMBEDDED}*

Network theory can be applied to most kinds of complex self-organising systems. These properties of being able to elucidate both the structure within complex systems and their metabolic scaling (Lentendu et al., 2014; Pawar et al., 2015) indicate that subnetworks, ecological networks and network theory could be widely applied to practical problems, including management and decision-making processes. Examples include the design of nature reserves or the preservation of ESs in urban planning, as well as the management of commercial marine fish stocks for human consumption. While the study of networks is embedded in theoretical ecology, the application of such approaches to managed ecosystems

has lagged behind. There are many reasons for this disconnection between pure and applied ecology, not least being the long-held pervasive view that human-managed systems (e.g., agroecosystems and commercial fisheries) are not only different from supposedly pristine ecosystems but that they are also fundamentally artificial and thus not “ecologically interesting” in a purely academic sense. This curious lack of investment in understanding the networks of managed systems is further highlighted by policy-driven environmental science tending to focus on disturbed or polluted ecosystems. Environmental policy thus exposes a general perception that natural systems, once perturbed, are somehow distinct from their natural counterparts. From this point of view, ESs provide a very suitable conceptual framework common to ecological science and policy and network theory is a valuable tool common to multiple disciplines. However, despite their increasing popularity, socio-ecological networks are still ignored in ES studies and the generation of appropriate and compatible data remains a crucial step for the quantitative estimation of ESs (Wallace, 2007; Feld et al., 2009).

5. Research priorities one decade after the Millennium Ecosystem Assessment

A priorities-listing exercise was designed to give a broad overview of research priorities for scientists and stakeholders, based on the expert knowledge of the co-authors, who represent a range of expertise across different disciplines and countries. We do not claim that this set of views is representative for the global situation, as any such survey is inevitably biased by the topic of expertise, geographical location, ecosystem type or other variables that cannot be controlled. Nevertheless, we aimed to collate and sift the views of this set of experts in the field to explore some of the major trends in the field since the publication of the MEA. The master list of headings we circulated is not exhaustive, but simply a broadly representative coverage of the main topics covered in the original MEA, divided into subheadings. The list was sent to a common pool of researchers by email and then discussed subsequently following receipt of the responses.

Responses were collated for groups of broad topical questions: a first block of 5 fundamental questions was derived from general trends in the existing literature (Figures 2 and 3), whilst a second block of 5 questions was more applied and narrower in focus. These two blocks reflected Holling’s basic functions (1987), given that exploitation, conservation and release have been mostly addressed within the supporting, regulating and provisioning ESs, whilst cultural services and constituents of human wellbeing were somehow the recurrent background beyond the second block (‘reorganization’). On average 182 words were added to the master list by each participant to define the “top-five” priorities. All the answers were aggregated within into a single file (repetitions due to the use of the same template text and associated references were removed).

A striking pattern is that all the replies are reasonably evenly distributed across the original ten categories, although not sufficiently evenly to obtain an equal number of issues in each category. Screening the word cloud of all the text supplied by the participants showed a common focus on particular aspects (Figure 8). Due to the different ways used by different contributors to formulate the same issue, the overlap was often high and responses could be merged. During this phase, a new category (“*What is the role of global connections in ESs delivery, and how should this impact our management and understanding/prediction of future provision?*”) was added. Overall, we identified 36 key scientific issues that, if answered, we felt would drive future advances in the field ESs. The resulting issues (as bullets) are

discussed in the following part, starting with the more generic issues listed from subsection 5.1 onwards.

<FIGURE 8>

5.1. Underpinning knowledge - from functioning to services

Biodiversity (species richness and functional diversity) and ecosystem functioning are not independent, and the debate regarding the identification of crucial aspects of the relationship between them is still open (Tilman et al., 1997; Huston et al., 2000; Jax, 2010; Cardinale et al., 2012). Effects of dominant species (whether a certain community assemblage is necessary to form and support a given ecosystem) matter at several levels (Perrings et al., 1992; Ospina et al., 2012) and can question the amount of biodiversity needed to maintain a function or provide a service (Kleijn et al., 2015). The discussion as to whether we need phylogenetic *versus* taxonomic *versus* functional levels of biodiversity (Mouchet et al., 2010; Mouquet et al., 2012; Gerhold et al., 2015) is ongoing. Many recent papers have attempted to gauge whether phylogenetic diversity is a useful proxy for community assembly or functioning but it does not seem to be the case all the time. Network approaches to the question may give more emphasis on the impact of ecosystem complexity, with the structure of ecological interaction networks appearing as key to our understanding of the dynamic and the functioning of ecosystems (e.g., Thébaud and Loreau 2003; Fontaine, 2013). Despite the widespread non-linearity in relationships between biodiversity and ecosystem services (e.g., Bennett et al., 2009; Carpenter et al., 2009; Koch et al., 2009; Lester et al., 2013; Grêt-Regamey et al., 2014) that fuels debates on methodologies to quantify biodiversity and its spatial and temporal variations, ES is still clearly a useful conceptual framework to bridge the typically isolated disciplines of the social and natural sciences.

Figure 9 addresses the extent to what various ESs depend on biodiversity: How many species are “needed” for the service delivery? But which process rate is desirable, and at which scale? The table in Cardinale et al. (2012) has a set of comparisons of correlates of ESs with various measures of diversity, and the picture is much more mixed (cf. Mace et al., 2012). Given the large amount of available data, methods of statistical reduction have been rapidly replaced by interaction metrics and graph theory (Thébaud and Fontaine, 2010; Poisot et al., 2013), allowing to visualize the relationships between ecosystems and ESs in a more intuitive way. Networks enable the integration of metabarcoding and interactions in graphs (e.g., Ji et al., 2013; Pocock et al., 2015; Vacher et al., 2015, and references therein) and allow visualization when a single function or a group of functions are needed (or not) for a specific ES, a group of ESs or a category of ESs. Currently, estimation of global ES values remains crude (Naidoo et al., 2010) and collecting ES metrics varies enormously in cost and complexity (Naeem et al., 2015). ESs are at present still largely studied independently and networks will enable a complementary service-lead approach to map ESs onto functions rather than *vice versa*. In the following sections we have compiled the major sets of questions under umbrella terms (in bold) that group them together within a recognisable recurrent theme:

- **Scales (#1)**. Which spatial scale is important for which ES? How to choose the resolution and how to set the grid size of the underlying abiotic environment? What scales are relevant for ES *versus* other scales like animal movement or conservation management? Does the relationship between Biodiversity and Ecosystem Functioning

(B–EF hereafter) and services change across scales? What are the most appropriate spatiotemporal scales and resolutions to study the links between B and ES? How does regional habitat loss influence ES of local patches and how can we scale up the knowledge from B–EF experiments to management or global scale?

- **Trade-offs and synergies (#1).** What are the shapes of the B–EF–ES curves and how much redundancy does biodiversity provide? How few dimensions of ES can we measure: are multiple services correlated or orthogonal? When ESs interact, how do we cope with the non-linearity that ensues? Why do the most productive ecosystems (Douglas fir, redwoods, beechwoods, tidal and freshwater marshes, bamboo forests) typically have low plant diversity? Which ESs are strongly correlated with biodiversity and which are not? Can we use molecular techniques to quantify microbial diversity (DNA) and microbial functioning (RNA)?
- **Metrics.** Which biodiversity metrics are the best descriptors of service delivery? As power law functions can take almost any shape (saturating, linear, concave, convex) and exponents are easy to compare both across systems and within ecosystems, are allometric exponents suitable for comparison?
- **Dimensions.** What are the dimensions of biodiversity that most matter in the delivery of ESs? Are there different mechanisms driving relationship between biodiversity and categories of ESs? Must we weigh the impact of non-native species, for instance by proportionating invasive species on ESs (as in urban ecosystems) and/or is the regenerative capacity and redundancy of ES depending on seasonal changes in the ecosystem structure?

<FIGURE 9>

5.2. *Regulating services*

Mutualistic symbioses, commensalism, parasitism and amensalism (e.g., whereby parasites might change the animal behaviour and either contribute or impede the delivery of specific services) are of general importance to regulating services. A large number of studies have been dedicated to understanding how a single pathogen agent interacts with its host, without taking into account the role of the overall biotic environment. This reductionist approach of pathogenesis has however evolved considerably in the last decade, triggered by the development of network ecology (Hudson et al., 2006; Lafferty et al., 2008; Vacher et al., 2008) followed by that of meta-omics (Berendsen et al., 2012; Vayssier-Taussat et al., 2014; Hacquard and Schadt, 2015). The transition to a more holistic understanding of diseases has led to the recent emergence of the "pathobiome" concept, which represents the agent integrated within its wider biotic environment (Vayssier-Taussat et al., 2014). Our understanding of the relationship between network properties and disease regulation is still in its infancy (Vacher et al., 2015). The idea revolves around the fact that symbiotic interactions might be key for functioning (e.g., the black queen hypothesis in microbial communities) and, hence, for services (Carroll, 1988; Kiers et al., 2007; Jackson et al., 2012; Polin et al., 2014; Rapparini and Peñuelas, 2014). Regulating services delivered through different co-production

processes mostly benefit human wellbeing locally, although many regulating ESs are influenced by local-to-regional management and global changes (climate warming, pollution, landscape fragmentation) spanning multiple scales (Hein et al., 2006; Gill et al., 2015; Stephens et al., 2015). Overall, service diversity coupled to biodiversity seems to be a good and reliable predictor for the delivery of regulating ESs (Raudsepp-Hearne et al., 2010a). We grouped questions under emerging themes, as before:

- **Scales (#2).** How do we accommodate the more global scale that regulating ESs operate over with the more local scale of provisioning and cultural services? Under which circumstances can these be provided globally, without regard to location, and when are they location-specific? What are the implications for management of these differences? What is the minimal/maximal/optimal size of ecosystems in respect to different regulating ESs? What are the differences between vegetation types, such as different tree species, on the efficiency of service delivery? At which scale should we measure microbial community structure in order to predict ecosystem health?
- **Technological control.** To what extent can bioengineering or (non-natural) capital be used? Can bioengineering help to maintain the output/endpoint of regulating services in the depauperate biota of disturbed systems? Can we improve the use of microbial organisms for climate regulation and waste processing? What are the consequences of planting crops/trees for biofuel on adjacent and connected ecosystems and what are the consequences on ES dynamics?
- **Biological control.** What are the main biotic (community) drivers of disease control? How will rhizosphere microbial clusters (indirectly) interact with each other during plant competition, and will this create synergies (e.g., disease suppression) in relation to ESs? There seems to be—at least in aphids—a trade-off between assimilation of symbionts giving resistance to parasitoids *versus* resistance to predators: can pest control be enhanced, and can we manipulate that to assist these “pest controllers”?
- **Disease control.** Is there a relationship between the structure of the residential microbiota within a host and its susceptibility to disease? Is disease susceptibility accounted for by the presence of a few species or by the structure of the whole microbial community? How to use networks to highlight the specific microorganisms and/or the properties of the whole microbial community that regulate disease?

5.3. Provisioning services

Biodiversity is the outcome of countless ecological and evolutionary events that occur over many scales in time and space: when humans genetically modify organisms, changes driven by (often local) economic interests are added onto >10,000 years of both artificial and natural selection. Regardless of the way we may define “nature,” natural capital stocks are in some ways analogous to financial capital in bank accounts. For instance, the financial systems have a high modularity (Haldane and May, 2011), like trait-mediated networks (Figure 6C). Whilst it is possible for us to extract high yields of resources from (natural and managed) ecosystems, if more than the interests yielded on that capital become extracted, then any system crashes (Raffaelli, 2016). The well-regulated forest management in many European

countries is a good stock-and-flow example of an ecosystem-yield approach that aimed for a sustainable timber provision. An example of one that is far less effective is that of the traditional species-centred (as opposed to ecosystem-based) approach to managing global commercial fisheries, which has been implicated in the crashes of many stocks around the world. Flows between domestic banks and across technological or biological networks are comparable, as shown by small-world similarities between financial, technological and biological models (Watts and Strogatz, 1998; Newman, 2003; Raffaelli, 2016). If these similarities are as general as suggested in the literature, constrained regularities can be identified and extended to ESs. Three main groupings of questions emerged under the heading of provisioning services:

- **Monitoring.** What are the best ways to monitor provisioning ESs, seen the low priority given to long-term change by governments and agencies? Can citizen science help us filling in the gap by bird-watching, butterfly counts, or vegetation surveys? Do alien species that are common in urbanized systems enhance provisioning services?
- **Modelling.** How can we model how harvesting of animals cascade through ecological networks affects other taxa and how important is the diversity of available resources?
- **Emergy.** Can stocks of natural capital and flows of environmental resources capture the full value of provisioning ESs within the concept of embodied energy (emergy)?

5.4. Supporting services

Urban systems are growing faster than any other land cover type (Meyer and Turner, 1992). Maintaining agricultural yield at a sustainable level requires that the regenerative capacity of driving subsystems is sufficiently strong despite fragmentation. Hence, economic trade-offs arise between management practices (e.g., conventional and no-tillage agriculture) and between rural and urbanized systems, and dealing with these has become a growing challenge. Large-scale anthropogenic disturbances, like the effects of nitrogen deposition on the diversity of mycorrhizal fungi (Chung et al., 2009; Cotton et al., 2015) and of atmospheric pollution in general on the genetic pool of pollinating insects (Gill et al., 2015), have also been investigated. The latter authors conclude that studies carried out during a single year may be difficult to generalise, as data across large environmental gradients and over long time spans are needed for a strong analysis, and these limitations apply to much of the field, where long-term large-scale empirical data are scarce (cf. Tylianakis and Coux, 2014). This makes the mechanistic interpretation of co-occurring ESs more difficult and a major challenge for future research, especially given the tendency for research funding to focus on short-term novelty, rather than monitoring the same set of model systems for many years (Text Box 2).

- **Trade-offs and synergies (#2).** What are the relative contributions of community biomass, species richness or trait diversity to biogeochemical ESs (e.g., hydrologic infiltration, soil stabilization, carbon sequestration, microclimate amelioration)? Why are some relationships between species diversity and productivity in natural ecosystems opposite of the relationships typically found in B–EF experiments?
- **Balance.** To what extent do ES-providing species or groups of species depend on non service-related species? Non-crop plants provide habitat and resources for pollinators, but can be a source of competition for resources (nutrients and light) and harbour crop

pests. How should pollinator habitats be managed to enhance populations but not be a major competitor for crops? Can we identify tipping points and can we exploit ecosystems to increase/manage their ESs? How can we balance agroecosystem ESs and trade-offs? How should a habitat be best spatially distributed for greatest gain?

- **Corridors.** What is the value of vegetated buffer strips to in-stream fungal leaf-decomposers, and how is the ecological quality influenced by non-managed buffer strips along surface water corridors (side effects of increased connectivity between land and stream)? What is the link between nutrient and toxicant removal by flooded riparian zones and the terrestrial vegetation that supports pollinators and other insects?

TEXT BOX 2 – BIODIVERSITY AND ECOSYSTEM FUNCTIONING: PRODUCTIVITY IN TERRESTRIAL ECOSYSTEMS

Services, especially in agriculture, can be strongly trait-mediated (Wood et al., 2015). If we consider the several types of plant–insect interactions (Fægri and Van der Pijl, 1979; DeAngelis and Mooij, 2005), a selective chemical pressure due to co-occurring direct effects of pollutants on plants and secondary effects of polluted hosts on their pollinators is likely to occur. Fægri and Van der Pijl (1979) introduced the so-called “pollination syndrome” to classify the pollination strategy according to the agents (wind or pollinators) by which pollen is transferred, and they showed that many insect-pollinated plants in agroecosystems have multiple pollination strategies, making them less dependent on a specific invertebrate, in contrast to plants in tropical forests and plantations. The trait-mediated disservices will be then different according to the geographical location of the site, as tropical ecosystems suffer the most by massive deforestation and landscape fragmentation and temperate ecosystems are often endangered by pollution. In a case study conducted in the Netherlands, the nectar-plants for butterflies were the only showing stress from heavy metals, whereas the nectar-plants for moths were the most tolerant to heavy metal pollution (Mulder et al., 2005). Hence, only the pollination service provided by adult butterflies was indirectly affected by pollution (but see Gill et al. (2015) for more case studies).

ESs are strongly influenced by shifts in land-use practices. Transformation of productive (species-poor) into less-productive (species-rich) grasslands remains a current practice in conservation and restoration ecology (Bakker, 1989). Such a transformation is a typical example of how some services are unpredictable in the soil: Wardle et al. (2004) coupled a relative fungal dominance in soils to nitrogen poor litter, although it is not always the case as shown by empirical evidence for effective competition between microbes and plants for nitrogen uptake (e.g., Setälä et al., 1998; Laakso et al., 2000). This phenomenon determines the structure of entire ecological networks. In particular, the distribution and length of trophic links are essential in the categorisation of the food-web structure, and we may expect that by evaluating their trophic links ecological networks might provide a tool to better forecast supporting and provisioning ES. For instance, changes in weeds and invertebrates between the herbicide management of spring-sown maize, beet and oilseed rape, and winter-sown oilseed rape, and the herbicide management of genetically-modified herbicide-tolerant varieties was evaluated across Britain (Firbank et al., 2003; Bohan et al., 2011), and the trophic links between each prey species and consumer species were given a probability score and weighted by logic-based machine learning (Bohan et al., 2011; Pocock et al., 2015). Such metawebs demonstrate that the long trophic links deviated more from the community response than the short (often intraguild) links, as most functional groups were found not to overlap each other (Sechi et al., 2015). In general, processes, functions and services result from a complex interplay of (a) biotic interactions (e.g., Hines et al., 2015).

For example, the plant biodiversity (centre of the embedded figure) translates at the same time into changes in the aboveground (light, green) and the belowground (dark, brown) networks, each of which results in different processes (examples in the black boxes) that affect the system's output (here as productivity). Even wild microherbivores contribute to such biogeochemical cycles (Belovsky and Slade, 2000). Network-based approaches are required if we want to understand multiple ESs, allowing predictions to be made for more organisational levels. Furthermore, responses of interacting components to interacting drivers can be predicted using such frameworks. For instance, homeostasis of C:N:P ratios (the so-called Redfield Ratio) strongly changes the food quality by CO₂ enrichment (Loladze, 2002). All such biodiversity-induced changes will cause, both above- and belowground, structural shifts in ecological networks (e.g., Reuman et al., 2008; Scherber et al., 2010; Mulder et al., 2012, 2013; Eisenhauer et al., 2013).

Embedded Figure Legend: How above- and belowground multitrophic interactions may translate into ecosystem services. Most functional guilds (herbivores, omnivores, carnivores) of the detrital soil food web ("brown pathway") are mirroring those of the aboveground food web ("green pathway") in this conceptual graph. Their close synergy is shown by supporting ESs like nutrient cycling (decomposition, mineralization) and provisioning ESs like pollination, jointly determining the primary productivity of the entire ecosystem, here as system's output (top black box). Like in the aforementioned freshwater system, pesticides have, also in terrestrial systems, a wide range of repercussions for both the "brown" and "green" pathways in any food web. For instance, direct effects of fungicides on fungal pathogens living on the phyllosphere, hence belonging to the "green pathway", are often linked to indirect effects on rhizosphere fungi and mycorrhizae of the "brown pathway". {FIGURE EMBEDDED}

5.5. Cultural and aesthetic services

Network theory may improve knowledge of relationships between biodiversity and its functions on one hand, and driving subsystems on the other. This is also true for cultural ESs in general and "charismatic fauna" in particular, especially as the latter are often (but not always) towards the top of the food web. Cultural ESs tend to be fund-service (non-consumptive) in nature and are by definition subjective. If the endpoint is "to maintain beauty or scarcity" of a particular ecosystem, then monetization itself is not an issue *per se* that can be made operational in environmental or economic contexts. If the endpoint is to maintain or increase the price value of housing that overlooks a neighbouring ecosystem of aesthetic value, then monetization may be a useful economic proxy. To a certain extent, the values of some of these ESs seem to reflect the level of the local social organization (ES granted to a nation, provided to a community, and even to an individual): for instance, zoological and botanical gardens are known to positively influence the attitudes of the visitors (Williams et al., 2015). Probably therefore ornamental plants – almost always introduced – are more influential in this service provision than native plants. Interestingly "charismatic species" or totemic animals (e.g. the North American bald eagle) are often large, rare species high in the food chain, though there are plenty of exceptions; in general they could simply be defined as organisms whose presence causes emotional changes in humans.

- **Emotional value.** How can we do better than 'willingness to pay' to assess the relative value of these services, e.g., using information offered via social media? What are biases in 'offered' information via social media? What is the meaning of spiritual value(s)?

- **Historical preservation.** Are there similarities between the protection of cultural heritage (e.g., a church or a painting) and natural heritage (e.g., a national park or seashore)? What does “nature” mean and which parts are mostly appreciated? How is nature ‘used’ by mankind? Can we (and/or should we) monetise these values?
- **Graduality.** What is the best way to assess and monitor changes in cultural and aesthetic services? Can we define trade-offs where humans perceive a change in cultural/aesthetic ESs or is the threshold gradually reached? How quickly do humans get used/adapt to a decrease in cultural/aesthetic services of their home environments?

5.6. Synergies among services and multiple drivers - how can we quantify main effects and interactions among ESs and their drivers in the real world?

There is a need to increase the capacity to measure and model the factors that currently lack in ES assessments (the dispossessed, the incommensurable, the unquantifiable - *sensu* Daw et al., 2015). Lavorel et al. (2011) mapped ES delivery using plant traits and soil abiotics, showing that trait distribution across landscapes is helpful to understand the mechanisms underlying ES delivery. However, although some taxa played a more major role, would the same be the case in human-dominated systems? Moreover, the main ES categories “behave” differently. Provisioning ESs are typically based on stock-flow resources, unlike regulating and cultural ESs, which are typically fund-service based. How do we ensure we can capture these in the same way if interactions apparently change through time (Bennett et al., 2009)?

- **Stress.** How many dimensions of stressors are involved – e.g., is it always the large, rare species high in the food web that are the most strongly affected, as seems to be the case for climate warming, habitat fragmentation, acidification, and drought? Do certain combinations of stressors amplify or modulate the effects of others? Which services are likely to be diminished and which enhanced by climate change or the spread of invasive species? Can interactions persist even though one or more stressors (e.g., summer drought events, severe fires or pesticide run-offs) are temporary?
- **Traits.** Beyond mapping: we need to advance the science for analysing and projecting change in multiple ESs in location-based studies. Can we produce functional models of ES delivery that accommodate ecosystem condition, ecosystem change as a response to multiple factors, thresholds, and uncertainty, and that can inform management decisions? Can trait and species distribution databases be merged and can the derived trait distribution maps be used to predict multiple ES provisioning at large spatial scales?
- **Trade-offs and synergies (#3).** How can we improve tools for measuring and modeling joint behaviour of multiple ESs (trade-offs, synergies, etc)? What causes relationships between services to be either trade-offs or synergies? Are they caused only by response to the same driver, or are there cases where ESs are truly interacting through ecological processes? What steps can we take to either reduce or enhance these effects, for instance by manipulation of network structure?

5.7. *How are services linked in different realms?*

When valuing ES changes, we must account for the complexity and connectedness of ecosystems in order to enhance the accuracy of values across different layers (Wegner and Pascual, 2011). Supporting ESs are the foundation of provisioning, regulating, and cultural ESs (e.g., De Groot et al., 2002; Wallace, 2007; Naeem et al., 2009). This makes the linkage between categories of ESs and separate ecosystems (surely if they belong to different realms) difficult within the existing conceptual framework. Moreover, within the freshwater–marine–terrestrial realms connections between ecological processes can be fundamentally different, affecting coupling of ecological processes or linking of services (Krumins et al., 2013; Mancinelli and Mulder, 2015) and the importance of the aquatic–terrestrial ecotones has been well addressed (Polis et al., 1997, 2004).

But can we make sure that we will be able to identify and locate all the beneficiaries across such large domains, sometimes even across political borders (López-Hoffman et al., 2010)? Protected ecosystems are classical examples for large (transboundary) domains: such areas exhibit a large number of important and valuable ESs (biodiversity, fisheries, recreational), yet they protect also invasive species and often act as reservoirs (Pejchar and Mooney, 2009; Burfeind et al., 2013; Hiley et al., 2014). In some aquatic ecosystems, like peatlands, the protective role with respect to flooding is rapidly vanishing, and as a result the biodiversity and associated recreational and educational ESs are also decreasing (Lamers et al., 2015).

- **Holism.** How do trade patterns affect ecosystem management, and how do changes in ecosystems that accompany these trade patterns likely affect future ES delivery? In ES delivery should this impact our management and prediction of future provision?
- **Landscape planning.** To what extent can we use ESs for defence against flooding due to rising sea-level? Does land-sharing *versus* land-sparing better optimise ES delivery? As urban systems are “loose” in their energetics and flows, would that evidently cascade down to adjacent systems with unwanted consequences?
- **Tipping points and whole-system shifts.** Can we identify pinch points (such as the extent to which freshwater fisheries of migratory species, like salmon, are dependent on coastal fisheries)? What is the importance of ontogenetic niche shift –turning one ES provider into another, or turning a neutral process into an ES provider?

5.8. *How do we prioritize the "value" of services?*

Scaling can be a problem for provisioning, regulating, and sustaining ESs, but not necessarily from a biophysical and mathematical perspective. Identifying the conditions that enable important changes, the drivers, what is reversible and what is not in ESs (cf. Davies et al., 2014), is now an urgent concern. An effective currency for measuring ESs in standardised and comparable ways will be a key issue (Howe et al., 2014; Bennett et al., 2015). It is a further concern that the value of some important ESs (“nature”) is difficult to quantify, but ESs should not be assumed to have zero value simply because they are harder to measure.

Valuing natural capital appears central to bringing conservation into the mainstream of modern societies (Daily et al., 2009), but Palomo et al. (2015) show how quantity and quality

of delivered ESs depend on different kinds of capital, which will also create different trade-offs that affect ES sustainability (Bateman et al., 2011; Reyers et al., 2013). Wellbeing may increase as certain ESs degrade (Raudsepp-Hearne et al., 2010b), but paradoxically it is also true that the environmental degradation reflects increased human wellbeing (at least in the short-term intragenerational scale). There are always winners and losers and we need to know more about who will win and lose where and when. This makes the prioritization of important ESs difficult, especially if we have to consider the social equity in rapidly growing economies (Pascual et al., 2014), but a focus on biophysical ES modelling approaches, such as in ARIES (ARtificial Intelligence for Ecosystem Services) leaves the translation of ES to economic values to the end user (Villa et al., 2014).

- **Values.** Can hypothetical (stated preference-based) and experimental valuation approaches (a form of non-monetary valuation based on choice experiments) *versus* people's revealed preference approaches, be a more effective means of valuing ESs with no direct monetary value, especially given intangible values such as cultural service values? Since ESs are always provided in bundles, does it make sense to value one ES, or should we only measure bundles of ESs? How can we realistically quantify ESs in terms of money including all hidden costs?
- **Priorities.** Can we prioritize ESs according to decreasing human needs and how does such a ranking change in different cultural/educational domains? Should values be based on the direct economic benefits for human society or adjusted according to the scarcity or vulnerability of the service impacted by human society?
- **Fairness.** How, when, and where are ESs co-produced by social-ecological systems? How to achieve fairness in the governance and policy instruments, such as Payments for Ecosystem Services (PES) to support the delivery of ES? How do ES values match with the notion of environmental fairness/justice which in turn is based on the institutional (both formal – such as policies- and informal – such as collective action norms and principles) settings? What are the culturally legitimate means of linking beneficiaries and providers to ensure ES delivery?
- **Trade-offs and synergies (#4).** How do we balance the values of benefits and burdens of delivering different services to different members of a community? What are the social trade-offs in ES, and what are the "injustices" and "inequalities" associated with the distribution of benefits and burdens of ES delivery? Why do lowland tropical regions with high biodiversity typically have more problems with disease, malnutrition, and human health than higher-elevation tropics and the temperate zone? How can equality of ESs be achieved in the face of gross global inequalities?

5.9. Coupling models to data - how do we develop a better predictive understanding?

Most data sets we currently have are heterogeneous and there are often strong limitations to their access (e.g., in the case of GMOs). But we need many more freely-available databases and the community urgently needs to continue building a universal open-source database for traits, records, services and trades. At the moment we have one huge annotated collection of all publicly available DNA sequences (Benson et al., 2013) and some smaller databases in

part available upon request, like that for vascular plant traits (Kattge et al., 2011). The stimulating suggestions of early investigations (e.g., Montoya et al., 2003) indicating relationships between food-web structure and the ESs provided by terrestrial ecosystems have been repeatedly confirmed, suggesting that food-web properties can explain some ESs not only across land-use systems (e.g., De Vries et al., 2013) but possibly even at much larger spatial scales (cf. Kissling et al., 2012; Hudson et al., 2014; Thomas et al., 2015).

Hence, land-use history matters in the ES delivery, making the urgency and the value of such a database greater. Even so, are there legacies of past provision that will matter in future provision? For example, the way that we harvest timber (how much, how often, how wide) can influence not only the immediate provision of other services (wild berries, carbon storage, greenery harvest for floral use), but the way services recover over time, which influences future ES delivery and, importantly, even future timber provision. While we know part of this pattern for some services in some locations, we are still far from having a general understanding of the role of legacies of past use on future ES delivery.

- **Data mining.** Can data on human wellbeing be incorporated to models to better predict the value of ESs? How do we incorporate abiotic factors as nodes into network theory? Do we have to distinguish between old and new stressors? How are ESs impacted by the increasing occurrence of extreme events?
- **Parameterisation.** To what extent can we exploit existing data to parameterise models? How complex do models have to be to get sufficient power, and how can we link terrestrial and freshwater models? Can we obtain better predictive understanding by using multi-faceted approaches?
- **Scales (#3).** What about the concept of multifunctionality? Do we accommodate scale dependencies when combining local-level data with global-level models? How much biodiversity can we afford to lose in future scenarios (2020, 2050, 2100) before services become unsustainable?

5.10. How can we manage systems for sustainable delivery of ESs?

We have to accept a continuous management of agroecosystems to obtain sustainable and deliverable ESs. A good example is that methods to produce food (such as ploughing and fertilizer use) can affect water quality now and, through accumulation of nutrients in the soil, also dramatically affect it far into the future, even after farming has ceased (Carpenter, 2005; Bennett et al., 2009). It will also be essential to improve communication and decision-support tools for public understanding of alternative options for managing multiple ESs (Mace et al., 2015).

- **Network of networks.** Does the concept “multiple ESs” make the issue too complex to be manageable? Given that biodiversity is distributed across spatial scales, should we identify and conserve “umbrella services” that will effectively promote services regulated by species at smaller spatial scales? And if so, how does the functioning of neighbouring ecosystems affect the delivery of a given ecosystem service?

- **Conflicts of interest.** How do we deal with trade-offs and conflicts of interest (e.g., shallow lakes rich in plants have clear water and high biodiversity – but may also be difficult to use for rowing and fishing)? What is the appropriate management unit to maximize the delivery of ESs across a landscape? How to optimize transboundary policies to protect ESs? How to deal with possible contrasting ESs in restoration projects? How can the health industry be persuaded that ecosystem restoration is cost-effective?
- **Stocks and flows.** How can the demand for ESs, and the way that it varies over space and time, be linked to the supply side analyses that ecologists most often undertake? ESs are “flows” that often depend upon a source, or a “stock”. How can we ensure that analyses incorporate stock depletion and its potentially non-linear impacts on service delivery? Can we quantify trade-offs by maximizing connectivity between (sub)systems (intragroup homogeneity) where possible and intergroup heterogeneity otherwise? Can we understand how trade-offs shift over time, with feedbacks, impact, etc.?
- **Scales (#4).** Can ES sustainability be managed at a local scale, or are large-scale approaches such as the catchment approach necessary? What are the policy instruments (e.g., payment for services) that would benefit both biodiversity conservation and ES delivery? How do we get workers from different disciplines to work together? How do we manage (or not) urban habitats as they return to a healthy state?

5.11. What is the role of global connections in ESs delivery, and how should this impact our management and understanding/prediction of future provision?

In an era of global connections (Liu et al., 2013, 2015), high-income countries meet demand for some ESs through international trade (e.g., Perfecto and Armbrrecht, 2003; Perfecto and Vandermeer, 2008), allowing them to protect biodiversity and ES delivery that are more easily produced locally and less easily traded (e.g., recreation). The exponential growth of global population and exponential economic growth (directly correlated with the growth of physical production of consumable goods) of countries such as China and India are driving an increase of the global human trophic level (Bonhommeau et al., 2013), also causing an intensification of the exploitation of marine food webs (Roopnarine, 2014). Such a worldwide increase is paralleled by a simultaneous “fishing down effect” (Pauly et al., 1998) of finfish species. Networks allow computing social, economic, and ecological aspects, making a focus on ES in different realms (marine, freshwater, terrestrial) possible, and examples of this application already being used in marine systems can be found in the EcoPath software widely used as a basis for gauging anthropogenic and environmental change on the production of commercial fish species within food webs.

- **Trade patterns.** How likely do trade patterns affect ecosystem management, and how will the environmental changes that often accompany these trade patterns affect future ES delivery?

- **Willingness to pay.** Do premium prices for food like coffee need to come exclusively from market forces? In other words, are consumers willing to pay higher prices to alleviate poverty, mitigate biodiversity loss and hence paying for ESs elsewhere?

6. Preliminary conclusions

Our 36 research priorities, as defined in the bulleted subheadings, are broad and diverse, yet there are some similarities among the questions and even across the topical categories: for instance, both the ‘scales’ and the ‘trade-offs and synergies’ subheadings are addressed four times. Regardless of the type of ES, most pleas and open questions address our concerns with dimensions. Spatial and temporal scales, stocks and flows, and costs and benefits are in fact nothing other than dimensional values in a particular unit. In addition, the plea for fine-resolution data reflects our concerns with defining appropriate dimensions. On the one hand, the coarser resolution of environmental grids derived from satellite imagery is appropriate to predict distributional shifts of species and ecosystems in response to climate change, invasive species and land overexploitation (e.g., Verbruggen et al., 2009; Pettorelli et al., 2014). On the other hand, studies aiming to understand microhabitats and local variables that vary over small geographic distances should use interpolated grids that are either fine enough to reflect properties *in situ* (e.g., Martínez et al., 2012) or remotely via the use of drones. As such, the choice of a specific unit is strongly linked to the available data resolution and the delineation of any service-providing unit is depending on the considered ES (Luck et al., 2003). As soon as we accept that different units will be appropriate for different groups of ESs, it will become possible to reach a broader and more workable consensus. From that perspective, the scientific community needs to provide the evidence for the appropriate units for any ES quantification.

Another issue, indirectly related to dimensions but directly reflecting ES quantification, is that of so-called ecosystem disservices (the negative or unintended consequences according to Pataki et al., 2011, or more simply the costs –being services the benefits– as in Escobedo et al., 2011). Losses of biodiversity or wildlife habitat, sedimentation of waterways, emissions of greenhouse gases, and pesticide run-off seem to be, for Power (2010) and Rasmussen et al. (2012), typical disadvantages of agroecosystems. Disadvantages seem to be widespread also in urbanized areas as the term ‘disservices’ is increasing in urban planning (Von Döhren and Haase, 2015). Interestingly, in ISI Web of Science the term ‘disservice’ seems to be used in Life Sciences twice as frequently as in Social Sciences and 4-times as much as in Health Sciences. There has been a tendency to study human–nature systems as separate entities and with unidirectional connections between human and natural systems (An, 2012), although the conceptualization of social-ecological systems is growing (Liu et al., 2007; Ostrom 2007, 2009). However, it is beyond the scope of this overview to delve further into the philosophical issues surrounding ESs.

Ecosystem services are on the rise in their use in environmental management. The traditional functional ecology point of view quickly evolves towards a societal-needs perspective rooted in the classical social sciences. This route of thoughts pointed out some open issues, and those in agriculture seem to be particularly challenging. Agriculture can be seen as the longest-running field experiment ever conducted, and understanding how artificial crop selection and land-use practices have moulded much of the Earth’s surface can help us gain a better picture of how to manage these complex systems to maximize the return of the goods and services they provide. It is becoming increasingly apparent that these systems are not the barren

monocultures they have long been assumed to be. Even oil palm plantations in the tropics and intensively-farmed arable fields in temperate regions, although they may not be as diverse as the surrounding habitats, possess complex interaction networks. Understanding these ecological networks could help us to assess unintended consequences of the loss or relocation of species and to improve sustainable management of our future ecosystems and also, ultimately, of the wider biosphere.

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FIGURE LEGENDS

FIGURE 1

The conceptual framework of Ecosystem Services (ESs) as presented by the Millennium Ecosystem Assessment (MEA, 2005). The arrows' widths and colours depict the supposed interaction strengths between Biodiversity and Ecosystem Services (left) and Human Wellbeing (right), although we should note that it has proved to be impossible to evaluate these interaction strengths in practice.

FIGURE 2

The number of papers published on the subject of biodiversity and ecosystem service(s) discovered in the Web of Science core collection ('biodiversity-ES') has been rapidly increasing over the past decade (black trend, secondary axis), which is much greater than the overall increase in the number of ecological papers published (gray trend, primary axis). Therefore the relative number of biodiversity-ES papers as a proportion of the total (number per 10,000 ecology papers; dotted line) still shows a marked increase. For reference the publication of the MEA is shown with a red vertical line.

FIGURE 3

The rapid temporal increase in scientific peer-reviewed publications (the Web of Science was accessed August 11, 2015); relative reference (100%) is the average of the number of papers in 2004 (one year before the Millennium Ecosystem Assessment) and 2005 (the boundary of the MEA is shown with a solid red line). Clockwise pies for each two years before the MEA (on the right) and after the MEA (on the left). Provisioning and regulating ESs (green, lower panel) are plotted on a logarithmic scale, supporting ESs (orange) and biodiversity (gray) are plotted geometrically (upper panel). More details in the text.

FIGURE 4

Temporal trends showing the cumulative growth of papers on landscape fragmentation (A) and rural intensification (B) for fragmented (C), independent (D) and mosaic landscapes (E).

FIGURE 5

Temporal trends showing the cumulative growth of papers on light pollution (A: rapid increase since 2005) and nitrogen deposition (B: less rapid increase after 2005 but more constant growth). Photo credits (left part): A) Radiance of the Earth by satellites, www.savethenight.eu, P. Cinzano and F. Falchi (University of Padova, Italy) and C.D. Elvidge (NOAA National Geophysical Data Center, Boulder, USA); B) Cluster analysis of ammonia deposition: the darker the colour the higher the NH₃ load (Mulder et al., 2015).

FIGURE 6

Examples of social, ecological and evolutionary networks. [A] Bipartite interaction network from Fortuna et al. (2013), reproduced from PLOS under the terms of the Creative Commons Attribution License. [B] Communication networks – (B₁) Directional network generated by Twitter interactions: Each node is a single user, orange edges represent mentions and blue edges represent re-tweets and exemplify according to Vespignani (2012) the co-evolution of two communities (reproduced with permission of the author and of Nature Publishing Group); (B₂) Cooperation network generated by scientific research: Each node is a single user, clusters exemplify common projects (giant component of scientists from Newman, 2006, defined as in Ma and Mondragón, 2012); (B₃) Repartition network generated by phone calls in a large urban space: Each node is a single user, geographical complementarities exemplify local communities inhabiting different parts of the city (Wang et al., 2015). [C] Circular networks – (C₁) Detrital food web from a natural grassland: Functional traits determine the modularity of the periphery (blue nodes) and the trophic links to the basal resources (green circles: fungi on the left, bacteria on the right) create two independent compartments ('Site F' from Mulder and Elser, 2009); (C₂) The "small-world" neural network of *Caenorhabditis elegans*, together with *Escherichia coli* and *Drosophila melanogaster* one of the most widely investigated organisms (raw data from Watts and Strogatz, 1998; rich-core method in Ma and Mondragón, 2015). The network methodology can be used to visualize ongoing processes and hence to exemplify ESs, even benefitting from the rapid development of molecular ecology (see Vacher et al., 2015 for more network examples).

FIGURE 7

Network of an empirical aquatic food web in Tuesday Lake, MI, USA, arranged according to trophic height (Cohen et al., 2003; Jonsson et al., 2005). In 1985 the largemouth bass, a top predator formerly absent from the lake but native to the region, was deliberately introduced as a part of the first trophic cascade experiment (Carpenter et al., 1987; Carpenter and Kitchell, 1993). We mapped from top to bottom the adverse effects of comparable alien species (Cohen et al., 2009) and possible non-target effects of a family of pesticides (carbamates) on specific trophic guilds. Each node (species) is split in three log-scaled components, the population biomass (white bar), the numerical abundance (grey bar), and the average body mass (black bar). From the lower trophic level: phytoplankton (potentially affected by algicides/or

herbicides), zooplankton (potentially affected by insecticides or molluscicides), and fish (sensitive to top predators). According to the schematical application of ESs to aquatic food webs (Brennan et al., 2014; Durance et al., 2015), cultural and provisioning ESs may be provided by top predators (e.g., recreational angling), and regulating and supporting ESs (e.g., carbon sequestration) tend to be restricted to lower trophic levels.

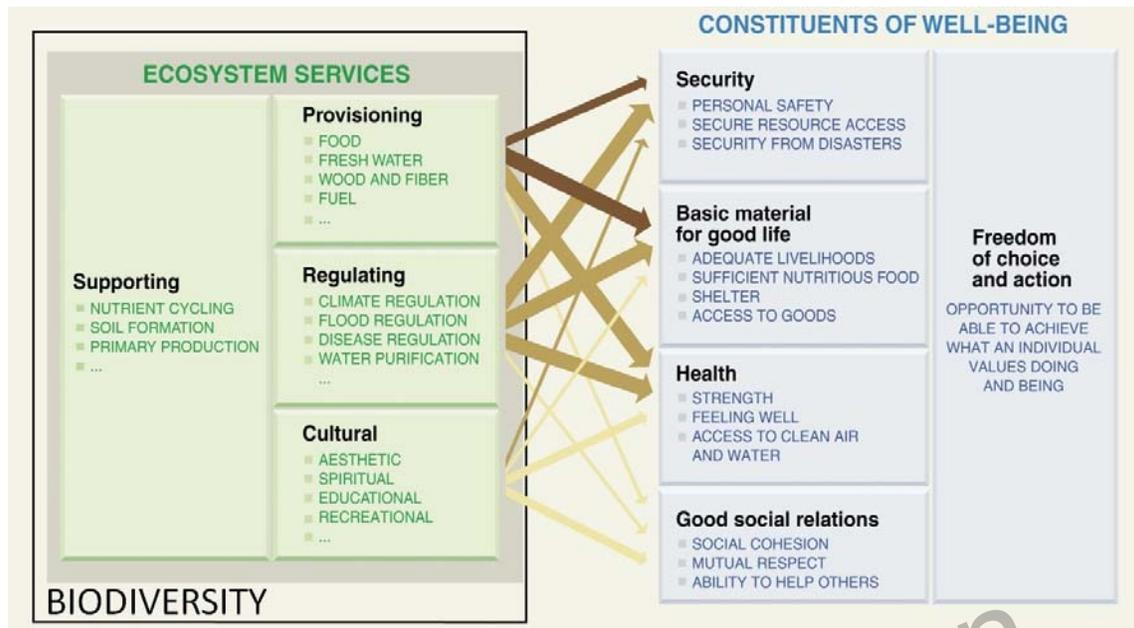
FIGURE 8

A word cloud generated from the research priorities collected during our internal survey. The cloud provides greater prominence (the numbers of entries determine the relative sizes) to the words that appear more frequently in the collated text. For instance, the word ‘service’ has been used 5-times as often as ‘biodiversity’ and the word ‘ecosystem’ has been used 2-times as often as ‘species’.

FIGURE 9

In a 10-ha experimental field near Jena (Germany), the number of vascular plant species were controlled and ecological processes were measured (Scherber et al., 2010). In that experiment, processes and ESs reacted rapidly to the initial increase in plant species diversity, after which some services like ‘weed suppression’ (here as inverse of invasion) tend to saturate while supporting services like ‘pollination’ and –to a lesser extent– ‘decomposition’ remain enhanced by biodiversity. Scherber et al. (2010) also exposed experimental nesting sites for wild bees and measured parasitism rates as proxies for occurring top–down control: parasitism rates increased with the number of plant species, resulting in potential biological control in species-rich ecosystems. (Figure recomputed with the original data by C. Scherber; photo credit W. Voigt.)

FIGURE 1



Accepted version

FIGURE 2

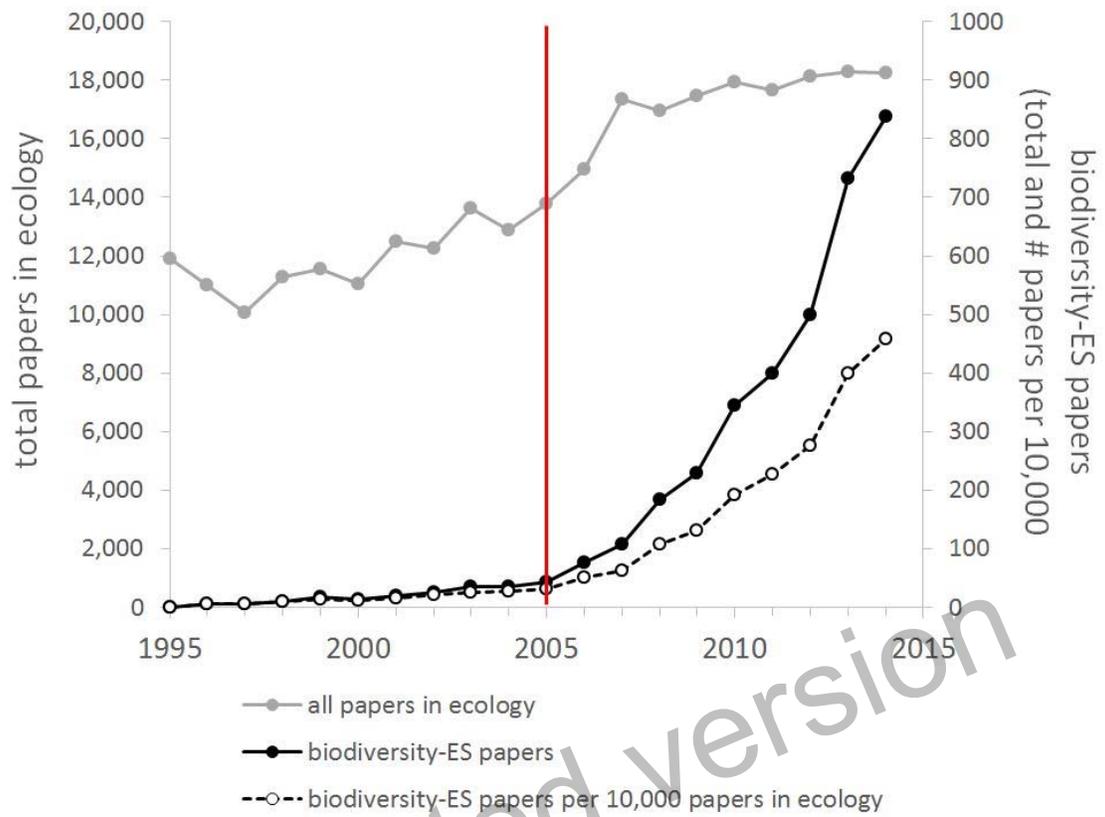
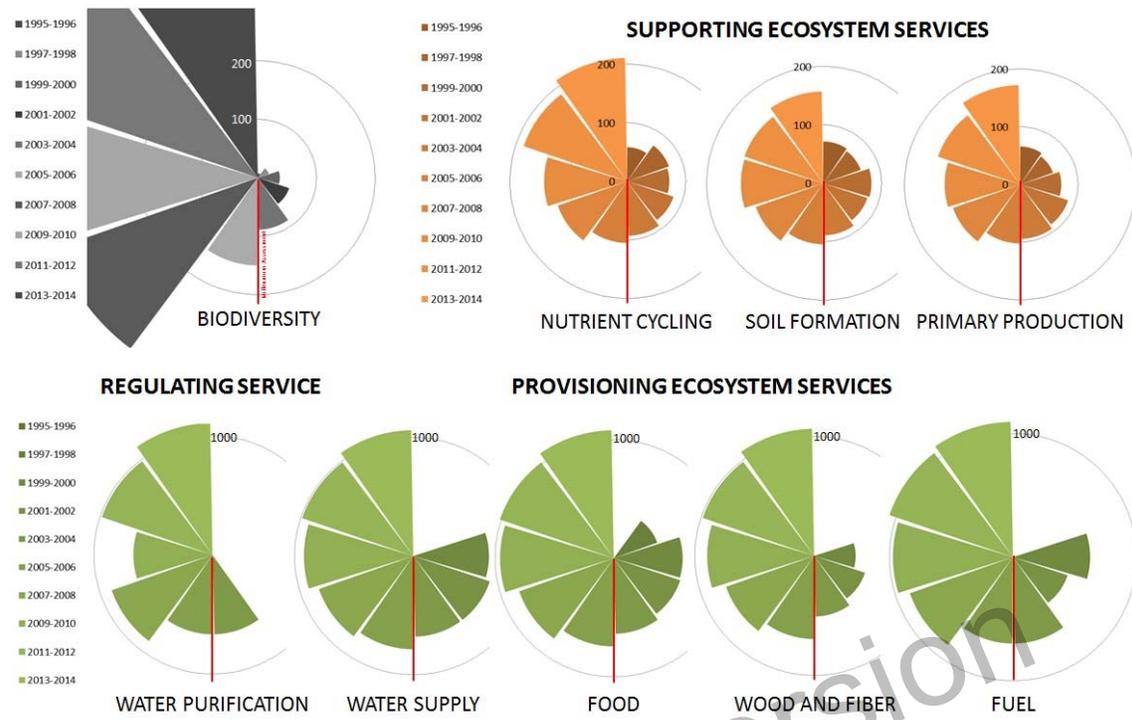
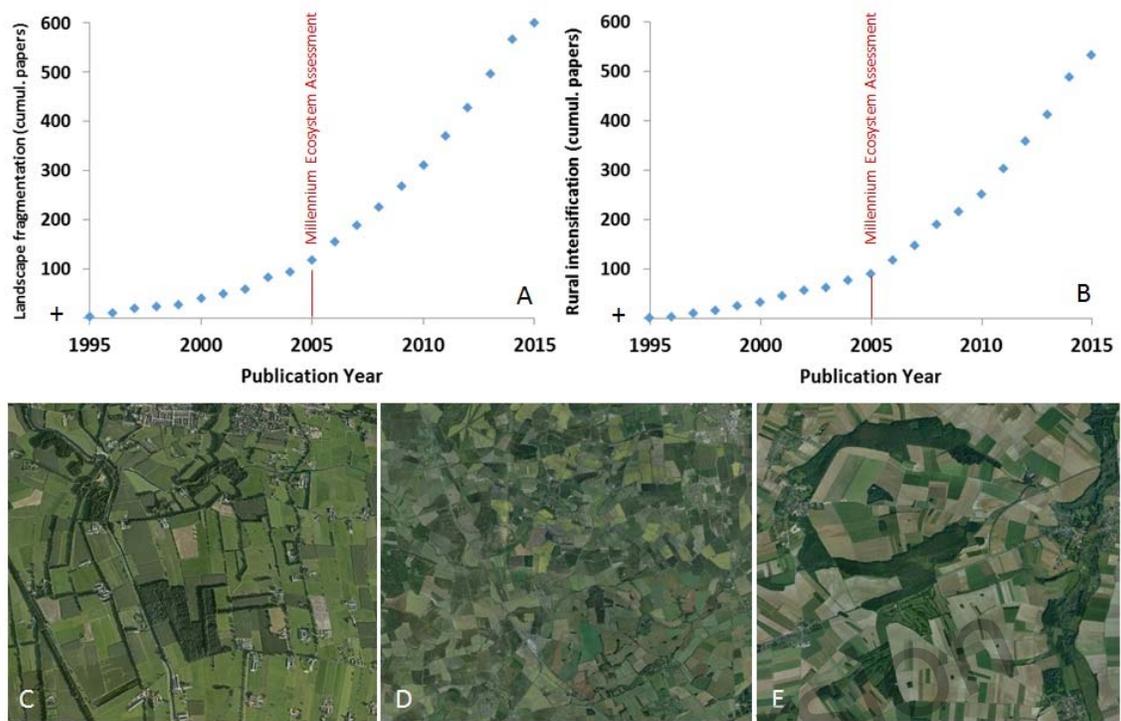


FIGURE 3



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FIGURE 4



Accepted version

FIGURE 5

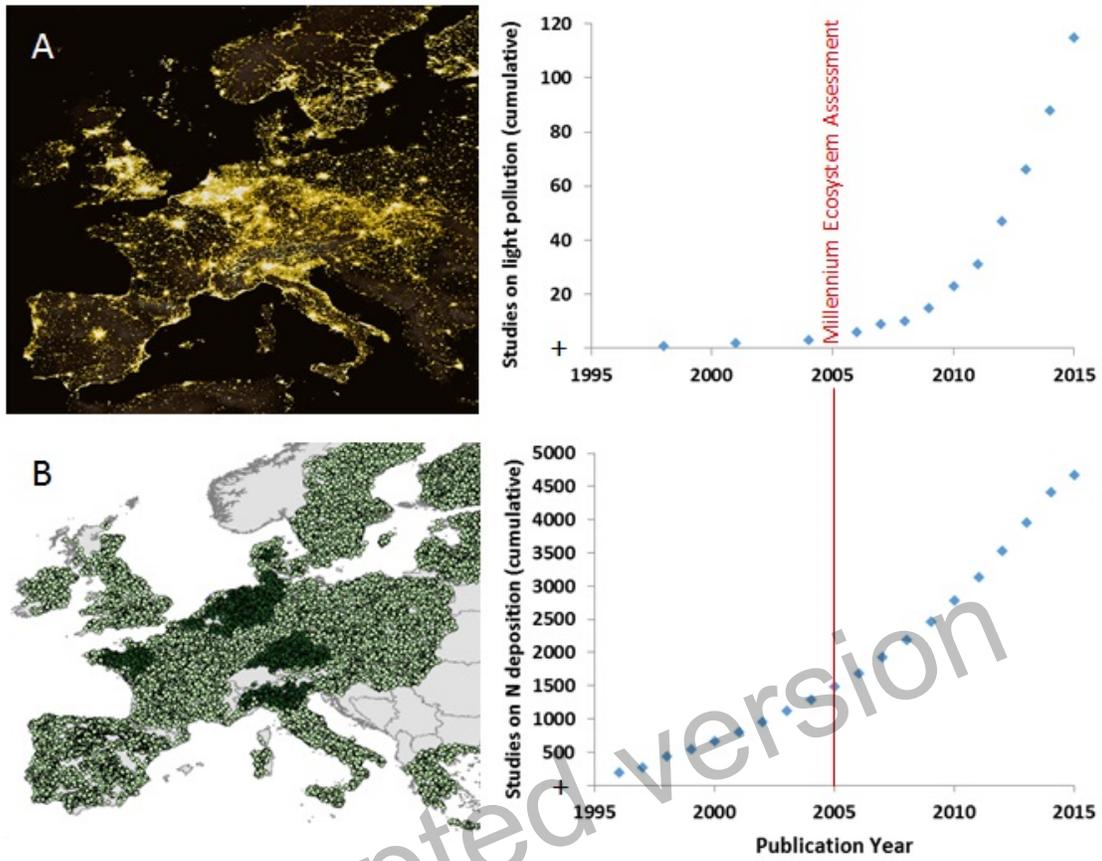
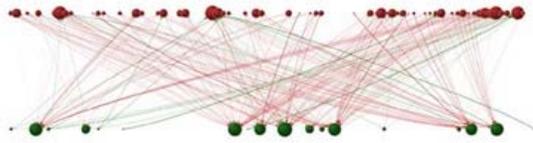
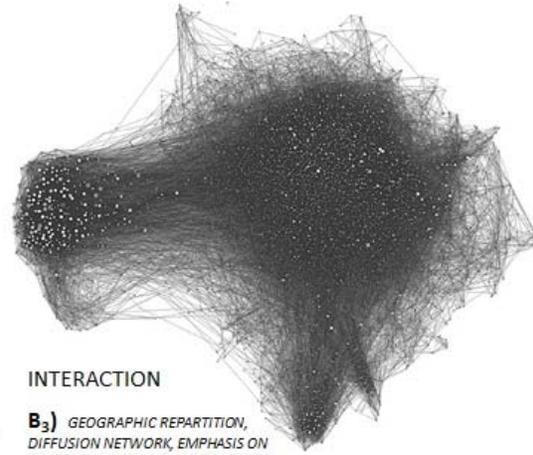


FIGURE 6

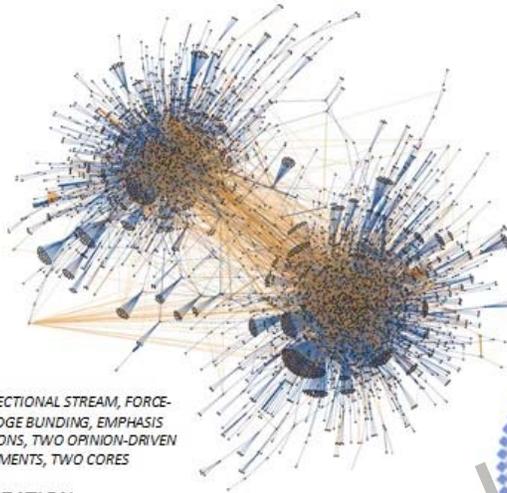


A) COEVOLUTIONARY-DRIVEN HOST COMPARTMENTS, CORES SHIFT IN TIME
SPECIALIZATION



INTERACTION

B₃) GEOGRAPHIC REPARTITION,
DIFFUSION NETWORK, EMPHASIS ON
COMPLEMENTARITIES, MORE CORES

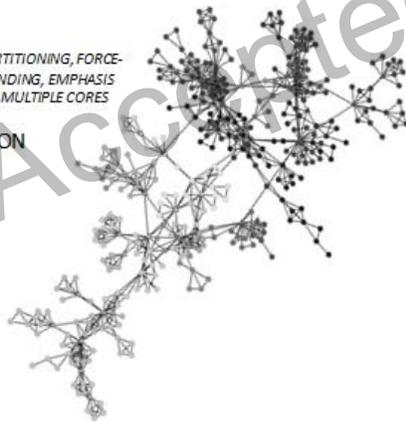


B₁) DIRECTIONAL STREAM, FORCE-
BINDED EDGE BUNDLING, EMPHASIS
ON DIVISIONS, TWO OPINION-DRIVEN
COMPARTMENTS, TWO CORES

POLARIZATION

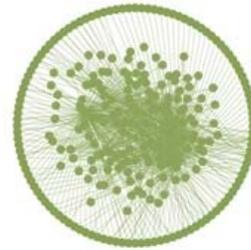
B₂) CLUSTER PARTITIONING, FORCE-
BINDED EDGE BUNDLING, EMPHASIS
ON SIMILARITIES, MULTIPLE CORES

COOPERATION



C₁) PERIPHERY SORTED BY SPECIES
MODULARITY, TWO RESOURCE-
DRIVEN COMPARTMENTS, NO CORE

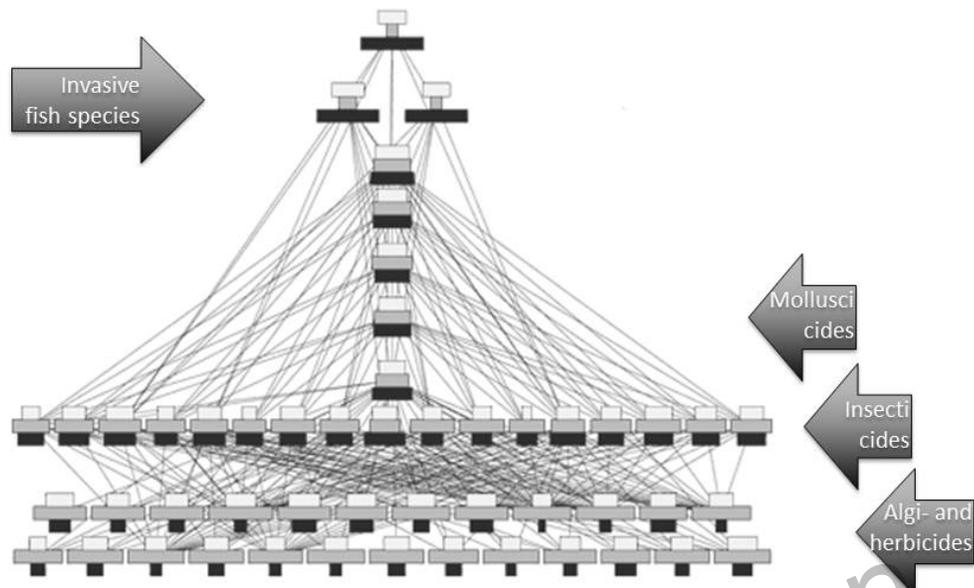
COMMENSALISM



C₂) CIRCULAR NEURAL PERIPHERY,
A LARGE CORE, STRUCTURE DERIVED
FROM THE RICH-CORE METHOD

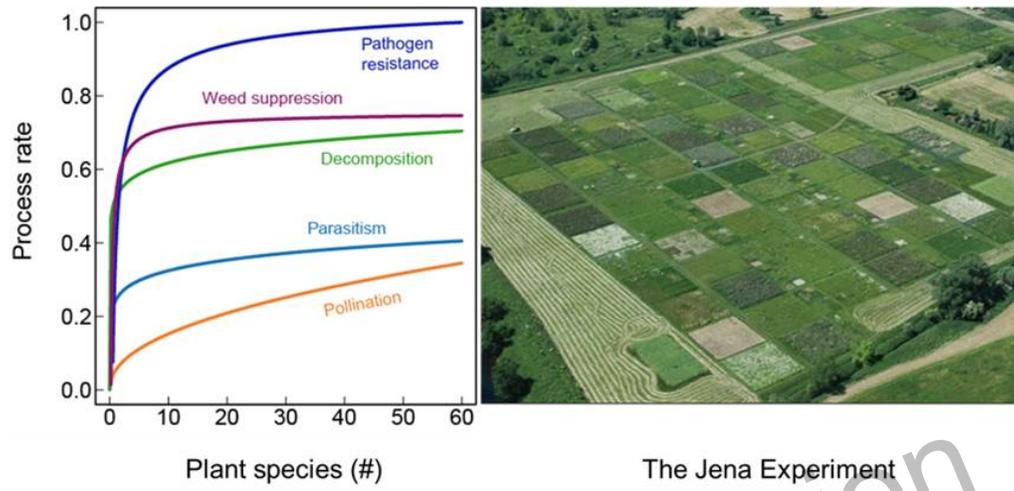
METABOLISM

FIGURE 7



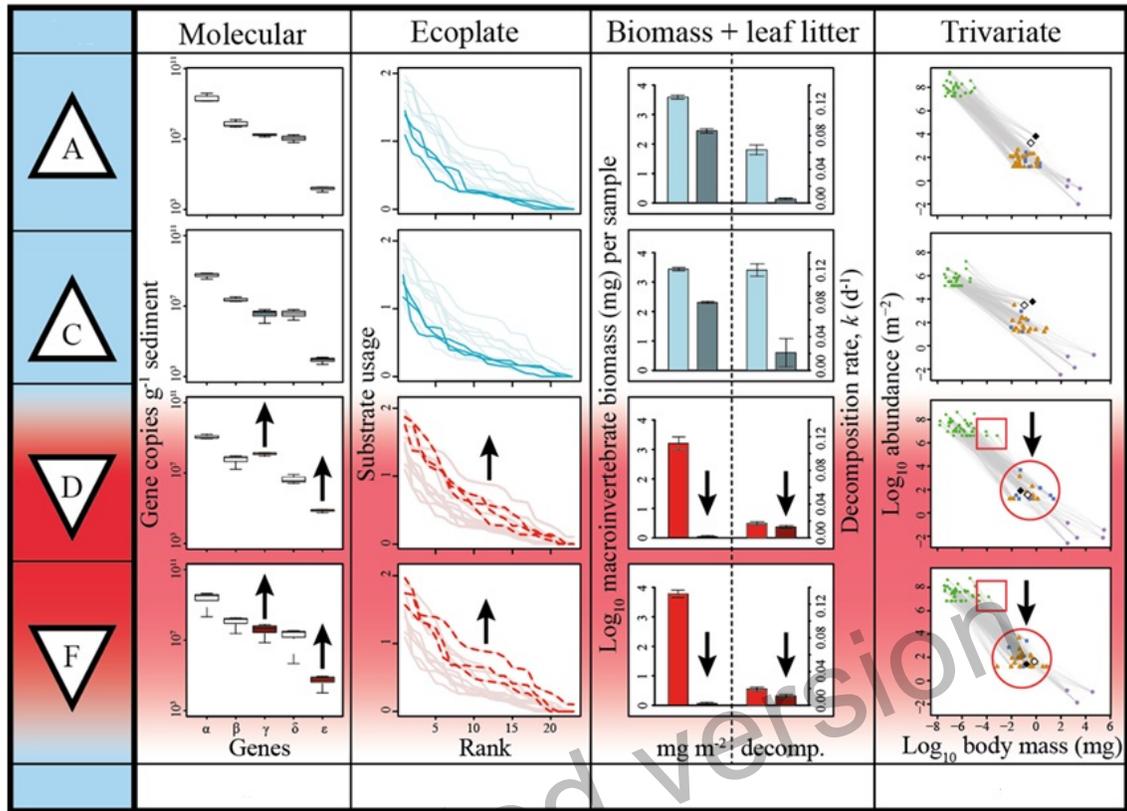
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FIGURE 9



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FIGURE TO BE EMBEDDED IN TEXT BOX 1



Accepted Version

FIGURE TO BE EMBEDDED IN TEXT BOX 2

