





Evosystem services: an evolutionary perspective on the links between biodiversity and human well-being

Daniel P Faith¹, Susana Magallón², Andrew P Hendry³, Elena Conti⁴, Tetsukazu Yahara⁵ and Michael J Donoghue⁶

A framework for exploring regional-scale trade-offs among ecosystem services and biodiversity protection has been established for some time, and it is clear that optimizing these trade-offs provides a strategy to address targets for a reduced rate of biodiversity loss. Recent trade-off studies have highlighted the need for better biodiversity measures, to complement measures of ecosystem services. Biodiversity typically has been linked in this context to existence and other non-use values. We argue that biodiversity will have a stronger role in such trade-off analyses if measures of biodiversity better reflect additional current and future services. These 'evosystem' services' have been, and, if we are careful, can continue to be provided by the evolutionary process. Some services have been provided through evolution operating in the past, and a phylogenetic diversity measure can help us to quantify these current and potential future benefits derived from the tree of life. Furthermore, a variety of evosystem services are delivered through ongoing contemporary evolution, and value should therefore be placed on the maintenance of healthy evosystems. We argue that the concept of evosystem services could be useful as a complement to the traditional concept of ecosystem services. Together, these reflect a fuller range of the services supported by biodiversity, and thereby provide a sounder basis for conservation planning and decision-making.

Addresses

 ¹ The Australian Museum, 6 College St., Sydney, NSW 2010, Australia
 ² Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, 3er Circuito de Ciudad Universitaria, Del. Coyoacán, México, D.F. 04510, Mexico

³ Redpath Museum and Department of Biology, McGill University, 859 Sherbrooke St. W., Montreal, Quebec, Canada H3A 2K6

Corresponding authors: Faith, Daniel P (dan.faith@austmus.gov.au), Magallón, Susana (smagallon@mac.com), Hendry, Andrew P (andrew.hendry@mcgill.ca), Conti, Elena (ContiElena@access.uzh.ch), Yahara, Tetsukazu (tet.yahara@gmail.com) and Donoghue, Michael J (michael.donoghue@yale.edu)

Current Opinion in Environmental Sustainability 2010, 2:66-74

This review comes from a themed issue on Terrestrial systems Edited by Anne Larigauderie and Harold A. Mooney

Received 16 December 2009, accepted 15 April 2010

1877-3435/\$ - see front matter © 2010 Elsevier B.V. All rights reserved.

DOI 10.1016/j.cosust.2010.04.002

Introduction

In this paper we argue that an evolutionary perspective is essential for developing a better understanding of the links between biodiversity and human well-being. We outline the services provided by evolutionary processes, and propose a new term, 'evosystem services', to refer to these many connections to humans. We have chosen this term intentionally to prompt comparisons and contrasts with the well-known concept of 'ecosystem services' [1,2]. The idea of ecosystem services has already been useful. Clearly, it helps people to understand the connection between the maintenance of healthy ecosystems [1] and their key services to humans: provisioning of the basics of life (food, wood, etc.), regulating the earth system (climate, water, etc.), and providing cultural elements (beauty, education, etc.). We believe that the idea of evosystem services could prove equally useful. Just as maintaining healthy ecosystems ensures the availability of clean water and other ecosystem services into the future, maintaining healthy evosystems will ensure that other crucial services are available into the future. 'Evosystem services' provides us with a useful handle in reflecting values that are not very naturally accommodated by the concept of ecosystem services, including the capacity for future evolutionary change and the continued discovery of useful products in the vast biodiversity storehouse that has resulted from evolution in the past. In this sense, 'evosystem services' and 'ecosystem services' are complementary. Together, the two capture a wider variety of the values that we associate with ecosystems and biodiversity.

The Millennium Ecosystem Assessment [2] distinguishes between ecosystem services and 'biodiversity' (all living variation, from the level of genes, to species, to ecosystems). While biodiversity is not considered a service per se, it is often seen as essential to the provisioning of ecosystem services (see also Mace *et al.* [3], this issue). While we acknowledge this distinction, we find the separation of biodiversity from the idea of 'services' to

⁴ Institut für Systematische Botanik, Universität Zürich, Zollikerstrasse 107, CH-8008 Zürich, Switzerland

⁵ Department of Biology, Faculty of Sciences, Kyushu University, Hakozaki 6-10-1, 812-8581 Fukuoka, Japan

⁶ Department of Ecology and Evolutionary Biology, Yale University, 21 Sachem Street, P.O. Box 208105, New Haven, CT 06520-8105, USA

be troubling, because we believe this might undermine support for biodiversity conservation. Here, we explore the idea that the value of biodiversity conservation can be made even more apparent through consideration of the evosystem services that it maintains. Proper recognition of evosystem services can increase the weight given to biodiversity conservation in decision-making. The notion of evosystem services not only encompasses services that extend beyond currently perceived ecosystem services, but also helps to highlight the need for the measurement of overall biodiversity. We develop our argument by first examining why current conservation approaches, which incorporate ecosystem services, do not yet deliver all that we need to link biodiversity to human well-being.

Perspectives in the international year of biodiversity

The year 2010 is a benchmark for biodiversity science and policy. First, 2010 has been designated by the United Nations as the 'International Year of Biodiversity', with a key goal of increasing awareness of the importance of biodiversity for human well-being. Second, it marks the deadline for the 2010 biodiversity target, adopted in 2002 by signatories to the Convention on Biological Diversity (CBD), for 'a significant reduction of the current rate of biodiversity loss'. It is now recognized that the 2010 target will not be met [4-6], and discussions therefore have focused on how we might do better 'beyond 2010' [5]. New, post-2010, biodiversity targets will be considered in 2010, as part of a new Strategic Plan at the tenth Conference of the Parties (COP) to the CBD.

Discussion of new targets has highlighted the connection between ecosystem services and biodiversity. The CBD has suggested goals 'to avoid loss of biodiversity that would be irreversible, costly to reverse or have particularly dangerous implications for human well-being', and 'to ensure the continued provision of ecosystem services' [7]. An IUCN report on post-2010 targets [4] similarly suggested that new targets could focus on human benefits of biodiversity arising through ecosystem services. The UNEP/WCMC report on beyond-2010 targets [8] and the Nordic 'Biodiversity Beyond 2010' report (http://www. dirnat.no/symposium2010) also argued for new targets focused on healthy ecosystems.

These arguments reflect the view that protecting ecosystem services also helps to protect biodiversity. A Countdown 2010 report (http://www.countdown2010.net/ article/its-time-for-post-2010-choices) argued that 'It is much easier to explain to people how nature provides essential goods, like clean water, and use that understanding as a basis to protect species'. Similar arguments contrast the utility of ecosystem services, with harder-tosell, non-use (ethical, existence, and spiritual) values of 'biodiversity' [9].

Early criticisms of a focus on ecosystem services expressed concern that, while this might highlight the importance of specific components of biodiversity (biospecifics), it would not necessarily create support for protecting biodiversity overall [10]. Such doubts about simple synergies between ecosystem services and biodiversity persist, even as ecosystem services gain increased attention [11]. A recent review [12] (see also [13]) called for larger scale examination of the connections between biodiversity and ecosystem services, moving beyond the exploration of synergies in the 'usual localized studies'. The authors argued that broad-scale trade-offs are apparent: 'The general increase in provisioning services over the past century has been achieved at the expense of decreases in regulating and cultural services, and biodiversity' [12]. Similarly, Egoh et al. [14] concluded that 'while biodiversity is seen as underpinning and ecosystem services is seen as a way to justify biodiversity conservation, it is acknowledged that the match between the two is not strong.' Various recent studies [15–19] review similar findings on such trade-offs.

We believe that this understanding that there may be trade-offs between protecting ecosystems services and protecting biodiversity presents us with a key challenge in developing post-2010 targets. The challenge is to better measure biodiversity and its corresponding utility or service values, so that these can be placed squarely 'on the table' when considering trade-offs with ecosystem services. We suggest that the notion of evosystem services might help us to address this challenge. There is also a great opportunity here, because by more effectively balancing these various needs of society, we may be able to deliver a reduced rate of biodiversity loss [20,21].

Incorporating biodiversity and ecosystem services in trade-offs analyses

A framework for exploring balanced conservation planning associated with ecosystem services and regional biodiversity is well-established. This broad umbrella of 'systematic conservation planning' [22] includes approaches that evaluate scenarios in order to explore the trade-offs implied by alternative spatial and temporal allocations of conservation actions within a region — for example, allocating some places to ecosystems services and others to biodiversity preservation. Such planning also considers 'synergies' — opportunities for biodiversity conservation and ecosystem services in the same place [23].

The earliest case studies, in New South Wales, Australia [24,25], used multicriteria analysis to balance biodiversity conservation with the provision of services over the region. A critical element was a biodiversity model which provided a surrogate for overall biodiversity (note that such multicriteria analyses do not require that biodiversity values be expressed in economic terms). The set of selected localities was efficient in that places for biodiversity conservation complemented one another and had minimum overlap with places desirable for forestry production services. This efficient balance among sometimesconflicting objectives implied that a given regional forestry production could be achieved with a higher degree of regional biodiversity conservation (Figure 3 in [24]). Thus, such balanced spatial planning can result in a reduced rate of biodiversity loss (e.g. http://australianmuseum.net.au/ image/Figure-2010-regional-tradeoffs). It can also deliver large biodiversity co-benefits, for example, when selecting sets of low-cost localities for carbon sequestration [26], or when targeting payments to landowners for ecosystem services [27].

The Natural Capital Project and its 'Integrated Valuation of Ecosystem Services and Tradeoffs' tool (InVEST) [28] provide recent examples of such balanced planning methods that explore regional trade-offs and synergies among biodiversity and ecosystem services. On the basis of InVEST case studies, Tallis et al. [28] (see also [18,29]) echoed earlier regional trade-off studies in concluding that: 'Land use/land cover... patterns that generate greater ecosystem service production may not always lead to greater biodiversity conservation'.

One problem with such planning is that, while recent studies promote the principle of regional-scale trade-offs, general conclusions are hard to draw because 'biodiversity' has generally been based on only a small number of species. For example, Anderson et al. [30], in their case study for Britain, used only a few species to represent 'biodiversity'. Polasky et al. [31], in their Oregon, USA, case study, reported land use patterns that 'sustain high levels of biodiversity and economic returns', but their 'biodiversity' was just 267 terrestrial vertebrates species. Nelson et al. [32], in their Oregon, USA, case study, found little evidence of trade-offs between biodiversity and ecosystem services — but their regional study relied on only 24 species as a biodiversity measure. The general point is that we need to incorporate better surrogates for overall biodiversity.

A second problem is that biodiversity has been associated (often implicitly) in recent case studies with intrinsic or existence values, and not seen as a measure or indicator of utility or services provided. For example, the Natural Capital Project characterizes biodiversity as being about ethics and intrinsic value, not human uses [11,28]. The IUCN [4] consultation report reinforces this separation, seeking new strategies to 'Recognize the intrinsic, existence and non-use value and importance of biodiversity, as well as to maintain ecosystem functions and processes'. Rockström et al. [33] linked biodiversity to the idea of critical loss thresholds by arguing simply that 'massive loss of biodiversity [is] unacceptable for ethical reasons'. Other studies similarly restrict biodiversity to intrinsic or ethical

values [9] (see also www.ieem.net/docs/BES_IEEM_ 2010_Position_Paper_(web).pdf). Increased appreciation of trade-offs is certainly welcome, but we believe there is now a risk that overall biodiversity will not be reflected properly in trade-offs when it is only linked vaguely to intrinsic values.

These concerns invite fresh perspectives on how to ensure that biodiversity is measured, and weighted, adequately in assessing trade-offs. Below we argue that biodiversity can gain adequate status in such assessments only when it is better recognized as a provider of concrete benefits to humans, above and beyond its already-recognized contributions to ecosystem services or its intrinsic values. We believe that it will be helpful to recognize these benefits as 'evosystem services.'

Back to the future: evolutionary outcomes as a storehouse and a factory for services Biodiversity and utility

We have highlighted the contrast between conventional perceptions of utility associated with ecosystem services and non-use values typically associated with biodiversity. This contrast may account for the limited measures of 'biodiversity' in recent trade-off analyses. What would more effective biodiversity measures look like, and what values would they capture? Certainly, the choice of values will affect our measures. If biodiversity is just a 'feel good' issue, then representing a few selected elements of biodiversity in our studies may be all we need.

In contrast, we argue that biodiversity measures should include uses or services that might otherwise be ignored in considering trade-offs with ecosystem services. Because the pursuit of some ecosystem services can sometimes entail the loss of biodiversity, it is important to make sure that other uses arising from biodiversity also are measured. We think those other uses are extensive – they include not only known uses from known species, but also yet-to-be discovered uses from known and stillunknown elements of biodiversity (e.g. see [34]). These unknown uses are linked to so-called 'option values' (for review, see [35°]). The Millennium Ecosystem Assessment [2], in referring to biodiversity loss, argued that 'global loss is more a concern about long-term option values, and hence defines a critical knowledge gap that goes beyond current perceived services.' Option values refer to the idea that maintaining variety maintains our options to benefit from future uses of biodiversity. While the consideration of the values of biodiversity has historically included option values [35°], these values sometimes are neglected in applications. The Millennium Ecosystem Assessment [2] concluded that 'a general lesson is that poor measurement of biodiversity reduces the capacity to discover and implement good trade-offs and synergies between biodiversity and ecosystem services....Sometimes responses to this information problem

may neglect the difficult problem of finding surrogates for global option values'. Further, in recent studies, such considerations have been given little weight relative to ecosystem services [36,37], or have been dismissed as impractical: 'to maintain biodiversity so as not to foreclose the options open to future generations ... would entail a goal of no overall loss of biodiversity... we suggest this is unlikely to be achievable' (Mace *et al.*, this issue [3]).

To better understand and quantify the option values of biodiversity, we consider the evolutionary processes producing living variation [38]. We broadly define 'evosystem services' as all of the uses or services to humans that are produced from the evolutionary process. We capture this idea by referring to the evolutionary 'system' hence, 'evosystem.' While our use of the term 'system' in this context may at first seem odd, there is nothing illogical about connecting 'system' with 'evolution', and we note that 'evolutionary system' and similar phrases have a long history of usage (e.g. Maynard Smith [39] on the 'dynamics of the evolutionary system').

Evolutionary history as an indicator of evosystem services

Because evosystem services include known and unknown services, we need measures that act as surrogates or indicators of the many uses derived from overall biodiversity that cannot be measured directly. We can perhaps best communicate the idea of evosystem services by presenting one example of an evosystem services surrogates measure, and its quantification of uses or services. A variety of such surrogates might be devised, but we illustrate the possible applications by reference to one such surrogate. The phylogenetic diversity (PD) measure [40] provides a measure of current and future uses derived from evolutionary processes, as summarized in a phylogenetic tree. The PD of a set of taxa is equal to the length of the path spanning this set on the phylogeny. If we connect those taxa on the tree, PD measures how much of the tree has been traversed.

The use of PD in biodiversity conservation is based on the assumption that the more evolutionary history that is represented, the greater the variety of features or characteristics of organisms that is represented [40]. That is, high PD should also represent high feature diversity. Setting conservation priorities to maintain feature diversity directly incorporates option value — that is, by maximizing the retention of feature diversity we also maximize the retention of possible future uses. Here, phylogenetic pattern provides the surrogate information on potential uses — the greater the evolutionary history represented by a set of taxa, the more current and future evosystem services can be provided.

An example illustrates how PD measures evosystem services. Forest et al. [41°] conducted an experiment to evaluate PD as a predictor of useful feature diversity. They listed all the known human uses of flowering plants in South Africa's Cape Floristic Region, and asked 'if we did not know these uses, would maintaining the PD of this group have been a good strategy for keeping options open to find these uses?'

A given genus was labeled as 'useful' if it had at least one species found in the Cape and recorded in a database of useful plants. Forest et al. scored usefulness under three different categories: medicinal, food, and all other uses. One immediate finding was that knowledge of which plants were useful in one category was not a good predictor of which plants were useful under another category. Thus, protecting species with known uses would not be an adequate way to protect species with yet-to-be discovered uses.

The most revealing part of their study asked: 'how should we have designed a conservation strategy to preserve useful plants if none of these uses were known?' Forest et al. [41°] found that directly maximizing the number of protected taxa would be one effective way to save lots of uses. However, they determined that a more effective way would be to select taxa for protection so as to maximize preserved PD. For example, the genera chosen to maximize PD contained a higher number of useful genera (over all use classes) than did the same number of genera selected at random. The authors concluded that the best way to retain the storehouse of future uses in plants in the Cape region would be to maintain as much evolutionary history as possible.

The Forest et al. study illustrates how evolution has provided us with a vast number of known benefits, and also how biodiversity as measured by evolutionary history can indicate benefits that we do not currently recognize — unanticipated future uses. We can think of the existing plant taxa, by virtue of their evolutionary histories, as providing services corresponding to known foods, medicines, and so on, but it also provides us with a storehouse of currently unrecognized benefits, and the PD measure helps us to quantify these evosystem option values.

The gift that keeps on giving: evolutionary process as a factory for human uses

In preparing this paper, our discussions revealed that our Japanese colleagues' perspectives on benefits from nature did not translate naturally into the term 'services', but rather into the term 'gifts.' We found this alternative a very satisfying way to think about evosystem services. Evolutionary history, as a storehouse of yet-to-be discovered uses, provides the 'gift that keeps on giving,' in the sense that we are apt to discover hidden treasures for years to come. But this idea of the gift that keeps on giving applies even more directly to the ongoing evolutionary process itself. Evolution continually produces new and often improved 'solutions' as environmental circumstances change, and it thus has the capacity to provide new services and benefits (including new ecosystem services) to humans in perpetuity.

One illustration comes from recent work on 'rapid' or 'contemporary' evolution; that is, ongoing evolution on relatively short time frames such as years or decades [42,43]. Over the past few decades, native seed-feeding soapberry bugs in Australia have evolved longer mouthparts, permitting the species to effectively attack the large fruits of the balloon vine — a serious invasive weed. This shift to a new food source and the resulting rapid evolution of feeding traits has effectively provided a new mechanism of biocontrol [44]. Similar possibilities have been suggested for a suite of other native species responding to invaders [45]. Other services likely rendered by contemporary evolution include the persistence of species in the face of environmental change ('evolutionary rescue' [46,47]) and evolutionary improvements in production traits following changes in harvesting strategies [48].

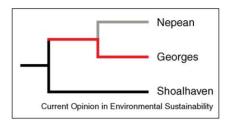
We have just highlighted beneficial outcomes of contemporary evolution, but there are clearly also cases in which rapid evolution presents challenges for humans. Consider, for example, the rapid evolution of resistance to antibiotics, or evolutionary changes that promote the more rapid spread of invasive species. These cases emphasize an important point — specific outcomes of evolution may well be judged as disservices, at least under current circumstances. Indeed, the issue of the nature of the correspondence between evolutionary outcomes and evosystem services becomes an open subject for research.

We have argued that evosystem services are delivered both from the storehouse of existing diversity, and via the evolutionary factory that is continually, and sometimes very rapidly, producing new solutions. These two aspects suggest a variety of strategies for conserving evosystem services. We may, for example, focus on the conservation of hotspots — places that uniquely represent evolutionary history [49]. We may also try to preserve places that may be engine rooms for future diversification, such as historically stable locations in the Atlantic Forests of Brazil [50]. Also, we may preserve genetic variation within species so as to maximize their future evolutionary potential (see Yahara et al., this issue [51]).

Integrating evosystem services into trade-offs and decision-making

To be useful for decision-makers, surrogates for evosystem services must provide indications of gains and losses. 'Complementarity' in biodiversity conservation reflects the gain (or loss) in biodiversity when an area is protected or degraded. Such values are regionally context depend-

Figure 1



Changes in PD contributions of localities. A schematic drawing of the phylogenetic trees derived by Baker et al. [52] based on gene seguence data for the mitochondrial cytochrome c oxidase I gene (COI). The taxa samples are labeled with the names of their river localities. The labels indicate the common phylogeographic pattern of variants within three taxonomic groups — the spiny crayfish (Euastacus), plus Atalophlebia (leptophlebiid mayflies), and Paratya (atyid shrimp). Human impacts on the Nepean River locality suggest loss of PD as shown by the gray branch length. The impacts also suggest that the unique PD contribution of the Georges River locality will now be greater, as shown by the red branch length.

ent — that is, they depend on the biodiversity retained in other places. A simple example of PD based complementarity values is illustrated in Figure 1. The PD calculations, based on the study of Baker et al. in eastern Australia [52], used a phylogenetic tree where the tips of the tree are labeled with their geographic distributions. In this case, the human impacts on the Nepean River locality and the resulting PD calculations indicated greater conservation priority for the Georges River locality.

The fact that the shift in PD-complementarity value for the Georges River locality was congruent over all of the observed taxa gives some confidence that this pattern may be valid for other taxa as well. This highlights a major challenge — the evosystem services contributed by localities will be most useful when the associated models allow statements that are relevant to many lineages in the region. In this context, it is interesting that the Baker et al. study used phylogenetic estimates from DNA sequence data. Their study illustrates how next generation sequencing technologies potentially can provide phylogenetic information rapidly and cheaply [51], over multiple taxonomic groups, even before formal names are assigned to any new species in the system. Example PD calculations [53] illustrate how such extensive new DNA sequence data may provide biodiversity surrogates, and help achieve the effective regional trade-offs that deliver a reduced rate of biodiversity loss [20,21]. Prospects for PD analyses of such data in relation to evosystem services are discussed further in Yahara et al., this issue [51].

Planetary boundaries, tipping points and biodiversity

Even before trade-offs among ecosystem services and biodiversity are considered, we may be able to identify critical thresholds — for example, a quantitative value for

a measure of biodiversity that we do not want to fall below. This idea is the basis for what Rockström et al. [33] call 'a novel concept, planetary boundaries, for estimating a safe operating space for humanity with respect to the functioning of the Earth System'. They defined boundaries as '... human-determined values of the control variable set at a 'safe' distance from a dangerous level (for processes without known thresholds at the continental to global scales) or from its global threshold. Determining a safe distance involves normative judgments of how societies choose to deal with risk and uncertainty'.

This approach has gained consideration in some post-2010 strategies. For example, the International Expert Workshop on the 2010 Biodiversity Indicators and Post-2010 Indicator Development [8] concluded that: 'Ecosystem tipping points and their possible consequences for human well-being should be considered and provide justification for targets and effective policy responses, on the basis of the precautionary principle'.

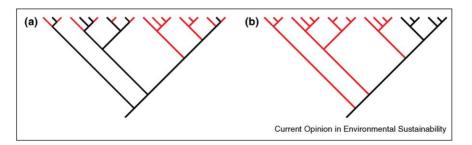
Rockström et al. [33] suggested a tipping point for the number of species extinctions, based simply on the argument that 'massive loss of biodiversity [is] unacceptable for ethical reasons'. How might consideration of evosystem services provide more defensible, objective, inputs to this kind of approach? First, evosystem service considerations suggest that tipping points based only on species numbers may be questionable. From an evosystem services perspective, losing a given number of species belonging to the same branch of the tree of life is not the same as losing the same number of species belonging to different branches.

A simple example (Figure 2) illustrates the disconnect between the number of species lost, and the proportion of evolutionary history lost. Yesson and Culham [54] used a phylogenetic tree for a plant group, Cyclamen, to examine PD losses under scenarios of climate change. They found high phylogenetic dispersion of those Cyclamen taxa with the lowest probability of extinction arising from potential climate change impacts. This pattern implied that the potential loss of PD and evolutionary potential through climate change was smaller than might be expected based only on species-counting. As Figure 2a shows, the six persisting, phylogenetically well-dispersed, Cyclamen species retain a large amount of PD. But now imagine that the exact same number of species persist, but are clumped in one part of the tree. Figure 2b depicts these hypothetical situations and illustrates that the loss of PD, for the same level of species loss, is much greater. This disconnect between species numbers and evosystem services suggests that tipping points based on species counts may have little utility.

There is also a positive message — perhaps the most natural manifestation of a tipping point can be found for these same phylogenetic trees and evosystem services. Tipping points may take into account longstanding pressures, with delayed impacts on biodiversity. Figure 3 provides a hypothetical illustration of what this means for the loss of evolutionary history (PD), as extinctions continue within a taxonomic group. The plot shows that successive species extinctions each may imply only a moderate loss of PD, until, abruptly, the last species goes extinct — and the long branch, representing a large amount of PD, is lost, A nominated 'boundary' could reflect the degree of acceptable risk to evosystem services relative to this tipping point. An approach called 'phylogenetic risk analysis' [55°] provides exactly this kind of risk assessment. For instance, one can study 'worst-case losses' that arise when one or more entire branches of the phylogenetic tree are lost. Phylogenetic risk analysis can guide decisions that try to reduce risk of these tipping point outcomes.

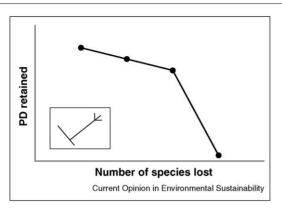
Currently, some authors are exploring boundaries and tipping points for one group, corals that are particularly

Figure 2



Loss of PD under climate change impacts. (a) Schematic drawing of the phylogenetic tree for cyclamens from the study of Yesson and Culham [54]. Red branch tips indicate species impacted by climate change and the six black branch tips are the relatively un-impacted species. The total length of black branches indicates amount of persisting PD, while the total length of red branches is lost PD. In this scenario, the six persisting species are phylogenetically well-dispersed, implying that a large amount of PD persists. (b) Schematic phylogenetic tree of a hypothetical contrasting result, where the same number of persisting species are now phylogenetically clumped. This implies that the loss of PD, for the same level of species loss, is much greater.

Figure 3



Phylogenetic diversity and tipping points. The plot shows the PD loss (vertical axis) as species are lost (horizontal axis) for a hypothetical phylogenetic tree (shown in inset), with three species at upper right side of tree, at the end of a long branch. Moving from left to right in the PD loss plot, loss of one species, and then loss of a second species imply small PD losses, but loss of the third species is a tipping point - the deeper ancestral branch and corresponding PD is now lost.

threatened by climate and land use changes. Carpenter et al. [56°] calculated that '32.8% of zooxanthellate corals fall into threatened categories, compared to approximately 25% of mammals and 14% of birds...If Near Threatened species are added, the proportion of corals (57.8%) exceeds that of all terrestrial animal groups assessed to date.'. These impacts on corals may be even greater at the phylogenetic level. While vulnerabilities to environmental changes are well dispersed on the phylogenetic tree (lots of diversity would persist), there are many examples where entire clades fall into IUCN threatened (or near-threatened) classes. On the basis of a large phylogenetic tree for corals [57], we can identify several cases resembling our simple example in Figure 3. For example, all listed species within Catalaphyllia, Physogyra, and Euphyllia are assigned to one of the threatened or near-threatened categories [56°]. The phylogenetic tree shows that these are the only descendents of a long branch. Thus, we have a situation in corals where conservation decisions can focus on the potential worst-case loss of this deeper branch (and the corresponding loss of evosystem services). Our conjecture is that similar risks associated with phylogenetic tipping points will be found in many lineages.

Conclusions

A core aspect of sustainability is the achievement of a good balance among the different needs of society [23]. We have argued that appreciation and quantification of evosystem (as opposed to just ecosystem) services can help ensure that biodiversity is properly taken into account in trade-offs and decision-making.

We have not really addressed the important question of the relationship between ecosystem services and evosystem services. In so far as all organisms and their features and interactions are products of evolution, it might be argued that ecosystem services are a subset of evosystem services. Another perspective is that the idea of evosystem services helps us to appreciate that ecosystem services have themselves changed over evolutionary time, as the components of these systems have themselves evolved and diversified. Our focus above has been on the use of the phrase 'evosystem services' as a tool to help us better account for all (or at least more) of the values associated with biodiversity. In this respect we view ecosystem services and evosystem services as complementary. We think that the notion of evosystem services can help us to better appreciate and measure the services provided by the tree of life and by healthy contemporary evolutionary systems. But, regardless of the exact terminology we adopt, our main argument is that we need fresh perspectives on biodiversity that help us to better represent the full range of uses and services in decision-making for sustainability. We believe that the phrase 'evosystem services' could prove useful in this context.

We close with a return to the discussion of prospects for a new CBD Strategic Plan [8]: 'The overarching goals of the Plan should be to promote the health of ecosystems in the interest of human well-being, to reduce the risks to human well-being from biodiversity loss, and to ensure options for future generations are maintained' (see also [58]). In this spirit, we have argued that human well-being is adequately safeguarded only when we appreciate the way in which it depends both on traditional ecosystem services and on the evosystem services that we have highlighted here. This perspective simply amplifies the last segment of the quote - the 'options for future generations' that evolution has provided, and will continue to provide, are critical in fully appreciating nature's gifts to human well-being.

Conflicts of interest

The authors declare that there are no conflicts of interest.

Acknowledgements

We acknowledge the support of the organizers of the second Open Science Conference of DIVERSITAS, held in Cape Town in 2009, and the funding provided by the Australian Research Council. We thank three anonymous reviewers, two guest editors, and our colleagues on the scientific committee for bioGENESIS for helpful discussions.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- Daily GC (Ed): Nature's Services, Societal Dependence on Natural Ecosystems. Island Press; 1997.
- Millennium Ecosystem Assessment. Washington, DC: Island Press: 2005.
- Mace GM, Cramer W, Díaz S, Faith DP, Larigauderie A. Le Prestre P, Palmer M, Perrings C, Scholes RJ, Walpole M et al.:

- Biodiversity targets after 2010. Curr Opin Sustain 2010,
- IUCN: 2010 is almost here now what? Consultation: options for a new vision for biodiversity; 2009 (http://cmsdata.iucn.org/ downloads/iucn_2010_options_paper_draft.pdf).
- Walpole M, Herkenrath P: Measuring progress towards the 2010 target and beyond: an international expert workshop on biodiversity indicators. Oryx 2009, 43:461.
- Fisher M: 2010 and all that looking forward to biodiversity conservation in 2011 and beyond. Orvx 2009. 43:449-450.
- UNEP/CBD: Revision and updating of the strategic plan: possible outline and elements of the new strategic plan. UNEP/ . CBD/SP/PREP/2 2009.
- UNEP/WCMC: Revision and updating of the CBD strategic plan: synthesis/analysis of views. UNEP/WCMC/Post-2010/ 0709/7; 2009.
- Armsworth PR, Chan KMA, Daily GC, Ehrlich PR, Kremen C, Ricketts TH, Sanjayan MA: Ecosystem-service science and the way forward for conservation. Conserv Biol 2007, 21:1383-1384.
- Faith DP: Biodiversity, biospecifics, and ecological services. Trends Ecol Evol 1997, 12:66.
- 11. Marris E: Biodiversity: putting a price on nature. Nature 2009, 462:270-271.
- Carpenter SR, Mooney HA, Agard J, Capistrano D, DeFries RS, Diaz S, Dietz T, Duraiappah AK, Oteng-Yeboah A, Pereira HM et al.: Science for managing ecosystem services: beyond the millennium ecosystem assessment. Proc Natl Acad Sci U S A 2009, 106:1305-1312.
- 13. Carpenter SR, DeFries R, Dietz T, Mooney HA, Polasky S, Reid WV, Scholes RJ: Millennium ecosystem assessment: research needs. Science 2006, 314:257-258.
- 14. Egoh B, Reyers B, Rouget M, Bode M, Richardson DM: Spatial congruence between biodiversity and ecosystem services in South Africa. Biol Conserv 2009, 142:553-562.
- Eigenbrod F, Anderson BJ, Armsworth PR, Heinemeyer A, Jackson SF, Parnell M, Thomasw CD, Gaston KJ: Ecosystem service benefits of contrasting conservation strategies in a human-dominated region. Proc R Soc B 2009, 276:2903-2911.
- Naidoo R, Balmford A, Costanza R, Fisher B, Green RE, Lehner B, Malcom TR, Ricketts TH: Global mapping of ecosystem services and conservation priorities. Proc Natl Acad Sci U S A 2008. **105**:9495-9500.
- 17. Wilson KA, Carwardine J, Possingham HP: Setting conservation priorities. Ann N Y Acad Sci 2009, 1162:237-264.
- Nelson E, Polasky S, Lewis DJ, Plantinga AJ, Lonsdorf E, White D, Bael D, Lawler JJ: Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. Proc Natl Acad Sci U S A 2008, 105:9471-9476.
- Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC: Conservation planning for ecosystem services. PLoS Biol 2006, 4:e379
- 20. Faith DP, Ferrier S: Good news and bad news for the 2010 biodiversity target. Science 2005; Online, 6 March (http:// www.sciencemag.org/cgi/eletters/307/5707/212#1272).
- 21. Faith DP: Global biodiversity assessment: integrating global and local values and human dimensions. Global Environ Chang 2005. **15**:5-8.
- Sarkar S, Pressey RL, Faith DP, Margules CR, Fuller T, Stoms DM, Moffett A, Wilson KA, Williams KJ, Williams PH, Andelman S: Biodiversity conservation planning tools: present status and challenges for the future. Ann Rev Environ Resour 2006, 31:123-159.
- 23. Faith DP: Biodiversity and Regional Sustainability Analysis. Canberra: CSIRO; 1995.
- Faith DP, Walker PA, Ive JR, Belbin L: Integrating conservation and forestry production effective trade-offs between

- biodiversity and production in regional land-use assessment. Conserving Biological Diversity in Temperate Forest Ecosystems — Towards Sustainable Management. Australian National University; 1994: pp. 74-75.
- 25. Faith DP, Walker PA, Ive J, Belbin L: Integrating conservation and forestry production exploring trade-offs between biodiversity and production in regional land-use assessment. For Ecol Manage 1996, 85:251-260.
- 26. Faith DP, Walker PA, Margules CR: Some future prospects for systematic biodiversity planning in Papua New Guinea - and for biodiversity planning in general. Pacific Conserv Biol 2001,
- Barton DN, Faith DP, Rusch G, Acevedo H, Paniagua L, Castro M: Environmental service payments: evaluating biodiversity conservation trade-offs and cost efficiency in the Osa Conservation Area, Costa Rica. J Environ Manage 2009,
- Tallis H, Ricketts T, Ennaanay D, Nelson E, Vigerstol K, Mendoza G, Wolny S, Olwero N, Aukema J, Foster J, et al.: InVEST 1.003 beta User's Guide. The Natural Capital Project, Stanford; 2008.
- 29. Tallis H, Polasky S: Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. Ann N Y Acad Sci 2009, 1162:265-283.
- Anderson BA, Armsworth PR, Eigenbrod F, Thomas CD, Gillings S, Heinemeyer A, Roy DB, Gaston KJ: Spatial covariance between biodiversity and other ecosystem service priorities. J Appl Ecol 2009. 46:888-896.
- 31. Polasky S, Nelson E, Camm J, Csuti B, Fackler P, Lonsdorf E, Montgomery C, White D, Arthur J, Garber-Yonts B et al.: Where to put things: spatial land management to sustain biodiversity and economic returns. Biol Conserv 2008, **141**:1505-1524.
- 32. Nelson E, Mendoza G, Regetz J, Polasky S, Tallis H, Cameron DR, Chan KMA, Daily GC, Goldstein J, Kareiva PM et al.: Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front Ecol Environ 2009, **7**:4-11.
- 33. Rockström J, Steffen W, Noone K, Persson A, Chapin FS, Lambin EF, Lenton TM, Scheffer M, Folke C, Schellnhuber HJ et al.: Planetary boundaries: exploring the safe operating space for humanity. Ecol Soc 2009, 14:32.
- Smith SA, Tank DC, Boulanger LA, Bascom-Slack CA, Eisenman K, Kingery D, Babbs B, Fenn K, Greene JS, Hann BD et al.: Bioactive endophytes warrant intensified exploration and conservation. PLoS ONE 2008, 3:e3052.
- 35. Faith DP: Biodiversity. In The Stanford Encyclopedia of Philosophy, edn Spring. Edited by Zalta Edward Nwr . 2008 In: http://plato.stanford.edu/archives/spr2008/entries/biodiversity/.

Reviews philosophical work on biodiversity, including the basis of option

- 36. de Groot RS, Alkemade R, Braat L, Hein L, Willemen L: Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. Ecol Compl 2009, doi:10.1016/j.ecocom.2009.10.006.
- Secretariat of the Convention on Biological Diversity: Connecting biodiversity and climate. In Change Mitigation and Adaptation: Report of the Second Ad Hoc Technical Expert Group on Biodiversity and Climate Change; Montreal, Technical Series No. 41; 2009:126.
- 38. Futuyma DJ: The uses of evolutionary biology. Science 1995,
- 39. Maynard Smith J: A comment on the Red Queen. Am Nat 1976, 110:325-330.
- 40. Faith DP: Conservation evaluation and phylogenetic diversity. Biol Conserv 1992, 61:1-10.
- Forest F, Grenyer R, Rouget M, Davies TJ, Cowling RM, Faith DP, Balmford A, Manning JC, Proches S, van der Bank M et al.: Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 2007, 445:757-760.

This case study for a global biodiversity hotspot region demonstrates that phylogenetic diversity (PD) measures can provide the conservation decision-maker with biodiversity information distinct from that obtained at the species level.

- 42. Hendry AP, Farrugia TJ, Kinnison MT: **Human influences on rates** of phenotypic change in wild animal populations. *Mol Ecol* 2008, **17**:20-29.
- Hendry AP, Lohmann LG, Conti E, Cracraft J, Crandall KA, Faith DP, Häuser C, Joly CA, Kogure K, Larigauderie A, et al.: Evolutionary biology in biodiversity science, conservation, and policy: a call to action. Evolution 2010, doi:10.1111/j.1558-5646.2010.00947.x.
- Carroll SP, Loye JE, Dingle H, Mathieson M, Famula TR, Zalucki MP: And the beak shall inherit — evolution in response to invasion. Ecol Lett 2005, 8:944-951.
- Carlsson NOL, Sarnelle O, Strayer DL: Native predators and exotic prey — an acquired taste? Front Ecol Environ 2009, 7:525-532
- 46. Gomulkiewicz R, Holt RD: When does evolution by natural selection prevent extinction? Evolution 1995, 49:201-207.
- Bell G, Gonzalez A: Evolutionary rescue can prevent extinction following environmental change. Ecol Lett 2009, 12:942-948.
- Conover DO, Munch SB, Arnott SA: Reversal of evolutionary downsizing caused by selective harvest of large fish. Proc R Soc B 2009, 276:2015-2020.
- Sechrest W, Brooks TM, da Fonseca GAB, Konstant WR, Mittermeier RA, Purvis A, Rylands AB, Gittleman JL: Hotspots and the conservation of evolutionary history. Proc Natl Acad Sci US A 2002, 99:2067-2071.
- Carnaval AC, Hickerson MJ, Haddad CFB, Rodrigues MT, Craig M: Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. Science 2009, 323:785-789.

- 51. Yahara T, Donoghue M, Zardoya R, Faith DP, Cracraft J: **Genetic diversity assessments in the century of genome science**. *Curr Opin Sustain* 2010, **2**:43-49.
- Baker AM, Hughes JM, Dean JC, Bunn SE: Mitochondrial DNA reveals phylogenetic structuring and cryptic diversity in Australian freshwater macroinvertebrate assemblages. Mar Freshw Res 2004. 55:629-640.
- Faith DP: Phylogenetic diversity and conservation. In Conservation Biology: Evolution in Action. Edited by Carroll SP, Fox C. New York, NY: Oxford University Press; 2008:99-115.
- 54. Yesson C, Culham A: A phyloclimatic study of Cyclamen. BMC Evol Biol 2006. 6:72.
- Faith DP: Threatened species and the potential loss of phylogenetic diversity: conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. Conserv Biol 2008, 22:1461-1470.

Reviews and further develops strategies for probabilistic approaches to assessing loss of phylogenetic diversity, based on the PD measure. Provides corrected calculations for the EDGE (evolutionarily distinctive, globally endangered) approach and develops a general framework for phylogenetic risk analysis.

- 56. Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A,
 Chiriboga A, Cortés J, Delbeek C, DeVantier L et al.: One-third of reef-building corals face elevated extinction risk from climate change and local impacts. Science 2008, 321:560-563.
 Demonstrates how a combination of climate change and land use
- Demonstrates how a combination of climate change and land use impacts on corals, with links to IUCN red-list rankings. Supplementary material provides impact ratings for individual taxa.
- Kerr AM: Molecular and morphological supertree of stony corals (Anthozoa: Scleractinia) using matrix representation parsimony. *Biol Rev* 2005, 80:543-558.
- Norgaard RB: Ecosystem services: from eye-opening metaphor to complexity blinder. Ecol Econ 2010, 69:1219-1227.