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Variability in ecosystem service measurement: a pollination service case study

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Research quantifying ecosystem services (ES) – collectively, the benefits that society obtains from ecosystems – is rapidly increasing. Despite the seemingly straightforward definition, a wide variety of methods are used to measure ES. This methodological variability has largely been ignored, and standard protocols to select measures that capture ES provision have yet to be established. Furthermore, most published papers do not include explicit definitions of individual ES. We surveyed the literature on pollination ES to assess the range of measurement approaches, focusing on three essential steps: (1) definition of the ES, (2) identification of components contributing to ES delivery, and (3) selection of metrics to represent these components. We found considerable variation in how pollination as an ES – a relatively well-defined service – is measured. We discuss potential causes of this variability and provide suggestions to address this issue. Consistency in ES measurement, or a clear explanation of selected definitions and metrics, is critical to facilitate comparisons among studies and inform ecosystem management.

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The ecosystem services (ES) concept helps to highlight the critical role that ecosystems play in sustaining human life, and is a valuable tool for communicating the benefits of conservation and informing policies that govern the use of ecosystems and resources (Chan *et al.* 2006; Seppelt *et al.* 2011). Following publication of the Millennium Ecosystem Assessment (MA 2005), there has been considerable growth in research focused on understanding and quantifying ES (Vihervaara *et al.* 2010), including provisioning, regulating, and cultural services.

Consequently, ES are being integrated into environmental policy and are increasingly influencing decision making (Boyd and Wainger 2003; Daily *et al.* 2009). However, inconsistencies in the methods used to measure ES may cause problems when assessing related trends and drivers and applying these results to inform land-management decisions and achieve conservation objectives.

ES research is multidisciplinary, given that knowledge of interactions among ecological, economic, and social systems is necessary to fully understand the provision of ES (Nicholson *et al.* 2009). This can create problems when attempts are made to synthesize research on ES, because the concepts and metrics being used to quantify ES by researchers in different disciplines are often dissimilar (Polasky and Segerson 2009). Although accurate metrics and indicators of ES provision are needed (Layke *et al.* 2012), inconsistencies in measurement methods and the resultant consequences for ecosystem management have, for the most part, not been mentioned in the literature (but see Boyd and Banzhaf 2007; Seppelt *et al.* 2012). However, in a recent case study, discipline-specific dissimilarities in interpretation and application of the ES concept led to marked differences in assessments of the quantity and distribution of these services (Lamarque *et al.* 2011). These differences can, in turn, limit comparison among studies, prevent consensus on trends and patterns, and limit the effectiveness of ecosystem management strategies based on ES assessment (Daily and Matson 2008).

Here, we outline potential sources of inconsistency in ES measurement and provide evidence of this variability using a case study involving pollination services. Pollination is a key regulating ES and involves a clear

In a nutshell:

- Ecosystem services (ES) are increasingly being studied across multiple disciplines
- However, definitions of individual ES are inconsistent or imprecise, diverse methods are used to quantify the same service, and few researchers adequately explain why a certain metric or definition was selected for use in their study
- In 121 published studies of pollination services, 62 unique combinations of metrics were used to measure this ES, highlighting the current methodological variability
- Inconsistent ES measurements complicate attempts to compare results between studies; to ensure that the ES concept remains useful for scientists and decision makers, we recommend increased effort to consistently define and measure ES

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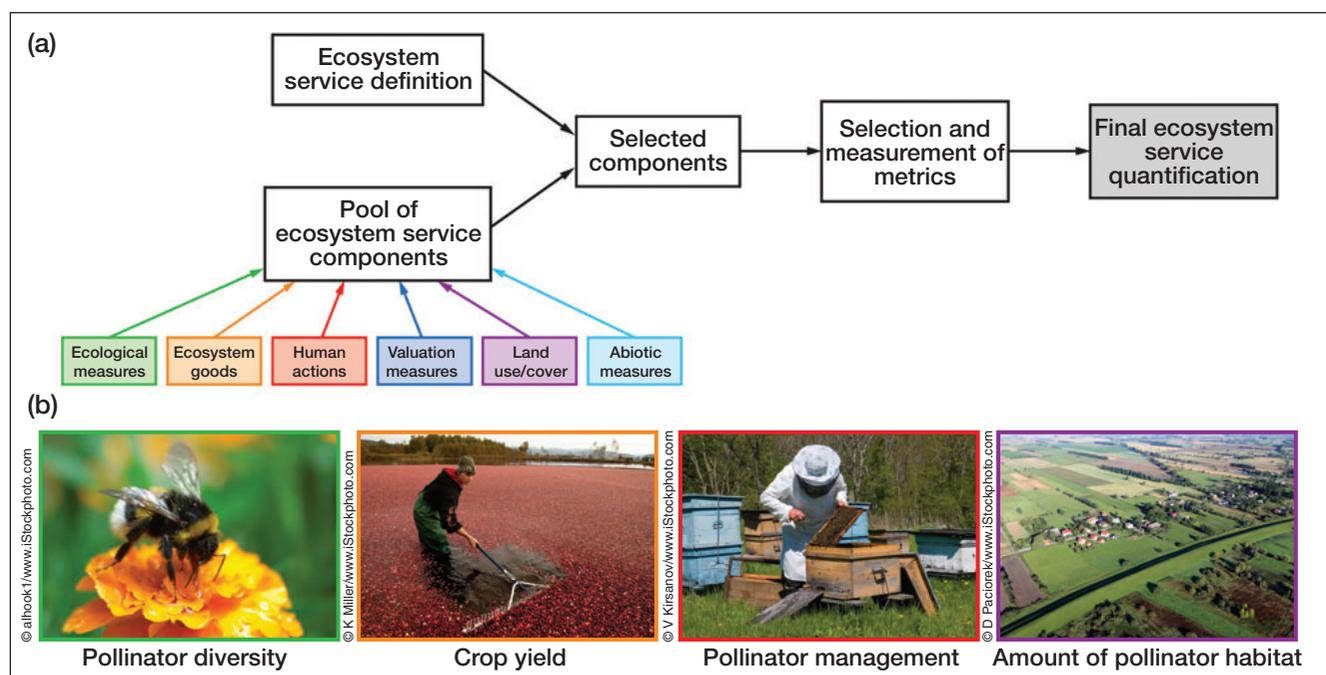


Figure 1. Measuring ES starts with defining the ES and the point where the benefit from an ecosystem is received. (a) The specific biophysical, social, and economic components that contribute to the chosen service definition are selected from a larger pool, and then metrics are chosen to quantify each of the selected components (Table 1). This includes ecological (green), ecosystem good (orange), human action (red), valuation (blue), land use/cover (violet), and abiotic (turquoise) components. The chosen metrics for each component are then measured and combined for final quantification. (b) For example, pollination services could be measured by combining metrics for pollinator diversity, yield of pollinator-dependent crops, human management of pollinators (eg domestic honeybees), and land cover of pollinator nesting habitat.

biophysical mechanism (pollen transfer enabling plant fertilization). It therefore has the potential to be measured more consistently than other services (eg flood regulation, spiritual values). We then discuss the challenges that this measurement-related inconsistency poses to ES research and suggest means of improvement. To our knowledge, this is the first formal analysis of how an ES has been quantified across studies. Our goal is to initiate discussion about measuring ES, as a first step toward improving comparability among studies and establishing protocols for measuring ES in diverse contexts.

■ Conceptual framework to assess ES measurement

We identified three common steps in the process of measuring an ES where researchers can introduce inconsistency: (1) defining the ES in the context of the study, (2) identifying the different components that contribute to that ES, and (3) selecting and quantifying a set of appropriate metrics to represent the chosen components (Figure 1). We use the term “components” to refer to the different biophysical, social, and economic constituents that collectively contribute to the production of an ES. Service production includes the biophysical supply of the service, its use by people, and the value attributable to that use (Tallis *et al.* 2012). Likewise, the term “metrics” refers to the set of actual measurements or data used to

quantify each component (UNEP–WCMC 2011). Each of these three steps involve decisions that can influence ES measurement methods and the final ES value. The first step establishes the researcher’s interpretation of the ES and what they aim to measure. The second step determines the components that contribute to service provision, based on the researcher’s ES definition. Finally, accurately measuring each component and determining the level of ES provision depend on choosing appropriate metrics to represent each of these components (UNEP–WCMC 2011).

ES occur where and when humans receive a benefit from the environment, but there is rarely consensus on the exact point where that benefit is realized (de Groot *et al.* 2010). For example, is food production a service when the crop is fully grown, when it is harvested, when the farmer receives payment, or when food reaches the table? By identifying the delivery of a benefit from the environment to people, an abstract ES becomes measurable. This point of delivery determines the ES “definition”, which can differ even between studies of a single service. Studies of pollination services, for instance, variously identify the benefit as: (1) the presence of pollinators, and consider the service to be “pollinator abundance” (Lonsdorf *et al.* 2009); (2) the deposition of pollen, and define the service as “pollen transfer” (Blanche *et al.* 2006); or (3) the production of food for human consumption from pollinator-dependent crops, and use the definition “food produc-

tion" (Ashworth *et al.* 2009), among other definitions. The ES definition, based on the researcher's perception of the benefit, will dictate what components are measured and what metrics are used to quantify them.

After an ES is defined, the components that contribute to its provision are quantified by metrics, each of which represents a quantifiable process or property. These components and metrics can be divided into broad categories: for instance, ecological variables, land cover, descriptors of human activity, and methods of valuation (Table 1). Tallis *et al.* (2012) emphasized the need to integrate measurements of ES supply (eg ecological variables), the use of the ES (eg human activity), and ES value, to capture the overall delivery of an ES. Where pollination services are defined as pollen transfer, for example, metrics include the rate of wild pollinator visitation and the number of pollen grains deposited (ecological component), the area of pollinator-dependent crops (land-cover component), and the cost of managing hives to replace wild pollinators (valuation component).

To combine all of these various metrics into a final value for ES provision, researchers use various strategies. One common approach is based on production functions (PF), where metrics are systematically combined through

the use of a detailed mathematical function (Barbier 1994; Tallis and Polasky 2009). This detailed approach aligns with the framework we have introduced here to assess ES measurement strategies, but the PF approach is not applied universally across ES science. Methods to combine ES metrics range from simple linear relationships and composite indices to the full PF approach.

■ Case study: measurements of pollination ES

To investigate variation in ES measurement, we reviewed how pollination services have been measured and classified these measurements according to our conceptual framework to assess measurement approaches (see previous section). We chose pollination because it is widely accepted as an important ES (Winfree *et al.* 2011), is highly studied, and is the subject of increasing attention and concern amidst declining pollinator populations (Bos *et al.* 2007).

Our review is based on publications found in ISI Web of Knowledge, SCOPUS, Agricola, and Academic Search Complete that included the terms "ecosystem service*" and "pollination" up to 15 Feb 2012. We aimed to capture all studies that self-identify as part of the ES literature and measure pollination services. We initially located 239 arti-

Table 1. Components and metrics for ES measurement

Component type	ES metric	Metric definition	Pollination metric examples
Ecological measures	Biodiversity	Species richness or functional diversity of species important for ES provision	Pollinator species richness; species richness of plants requiring insect pollination
	Species abundance	Abundance of species important for ES provision	Pollinator abundance; total number of pollinators visiting flowers; beehive size
	Ecosystem properties	Measure of a static ecosystem attribute at a single point in time	Fruit or seed set; flower density; seed or fruit mass; flower corolla length; pollinator foraging and nesting resources
	Ecosystem functions	Measure of an ecosystem flux of material or energy through time	Pollinator visitation rate; pollen transfer rate; fruit mortality rate
Ecosystem goods	Ecosystem goods	Physical products of an ES	Crop yield
Human actions	Policy decisions	Measurement of human decisions or policies that affect ES provision	Recommended hive densities for crop pollination; insecticide application regulations
	Human uses	Measurement of the human use of or demand for an ES	Amount of pollinated crop consumed; number of managed beehives
	Human inputs	Measurement of the human inputs that have taken place for society to receive the benefits of an ES	Pollinated crop harvesting and production costs; creation of flower meadows for pollinators
Valuation measures	Economic values	Monetary value of an ES or an ecosystem good provided by the service	Price for pollinated crops; total value of pollinated crops
	Non-economic values	Non-monetary value of an ES	Producer perception of the value of pollination for their crops
Land use/cover	Land use/cover	Spatial extent of different land covers or land-use types	Area of pollinated crops; area of pollinator foraging and nesting habitat; isolation of fields from natural habitat
Abiotic measures	Abiotic conditions	Environmental or physical conditions	Sandy soil for pollinator nesting; elevation

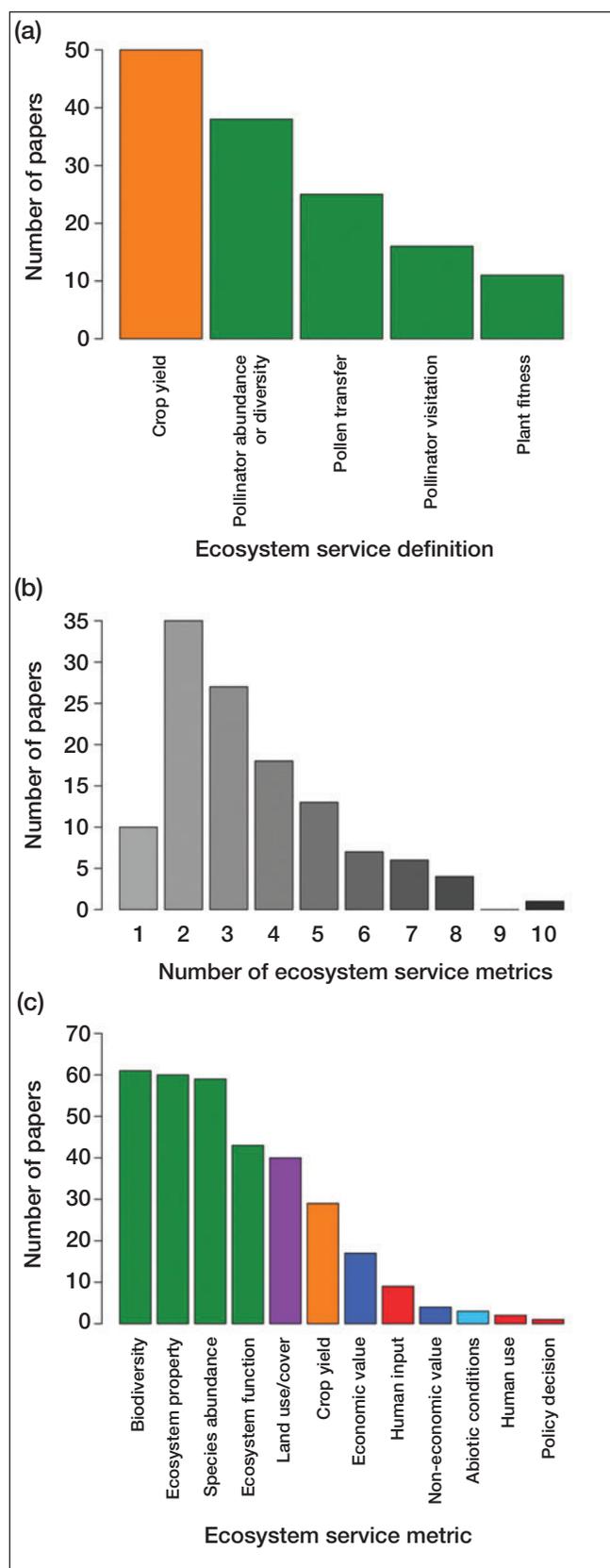


Figure 2. Studies of pollination services use (a) a wide variety of pollination service definitions, (b) various numbers of measurement metrics, and (c) different types of measurement metrics to quantify ES provision. Colors of different definitions and metrics are as in Figure 1.

cles but reduced this to 121 (see WebReferences) by excluding articles that did not explicitly measure pollination as an ES. We categorized these papers based on the authors' definition of the ES and the types of metrics used, according to our conceptual framework (Figure 1; Table 1).

How are pollination services defined?

Pollination service definitions varied across studies, but only 32% of papers provided explicit definitions in the context of the study being reported. Without an explicit definition, it is difficult to judge whether differences in ES provision between studies reflect actual differences in pollination services or subjective differences based on inconsistencies in identifying the point where benefits to people from the environment are realized (Hodges 2008). For papers without explicit definitions, we inferred definitions based on the units of the final measurement and identified broad pollination service definition categories across all of the papers.

The most common way that pollination was defined in the papers we analyzed was crop yield (41%), followed by pollinator abundance/diversity (31%), pollen transfer (21%), pollinator visitation (13%), and plant fitness (9%; Figure 2a). Categories were not mutually exclusive, and a single paper could include definitions that bridged multiple categories.

Defining pollination services as crop yield is problematic for several reasons. First, crop yield is often used as a measurement of another ES, namely food provision. By defining pollination services in the same way, we may be conflating a regulating service (pollination) with a provisioning service (food provision), thereby “double counting” the value of pollinators and food for human well-being. Second, measuring pollination services according to crop yield incorporates factors controlling yield that are unconnected with pollination. For instance, climatic conditions, irrigation, or fertilizer application could change crop yield while actual pollination remains static. Alternatively, management can be altered to maintain crop yield, despite decreased pollination services (Dale and Polasky 2007). By ignoring the contributions of these other factors, a study that uses only crop yield to quantify pollination may reach flawed conclusions about the state of the ES. If such a study is then used to inform management decisions or to implement policy, any subsequent recommendations may not be effective for maintaining or improving pollination services. The PF approach offers a possible solution by ensuring that the incremental contributions of various intermediate steps (eg abundance of pollinators, visitation rate, pollen transfer) are taken into account. However, in the studies assessed here, this was clearly not the dominant strategy used for pollination services, and there are cases when such an approach is not possible or appropriate.

How are pollination services quantified?

Within the studies we reviewed, 12 different ES metrics were used, representing six different ES components. The

range of metrics in a given paper spanned from one to ten, although most papers relied on four or fewer metrics; on average, pollination was most often measured using two metrics (Figure 2b). The metric that was used most frequently (50%) was biodiversity, and metric use was heavily weighted toward quantification of ecological components (Figure 2c). Overall, 62 unique combinations of the 12 ES metrics were used in the 121 studies. This means that, on average, fewer than two studies measured pollination services by the same combination of metrics, thus emphasizing the reported variability in pollination service measurement.

Metric use also depended on the pollination service definition (Figure 3). In general, metrics of human activity and valuation components (eg the cost to maintain beehives, or a change in the economic value of a pollinator-dependent crop) were more common when pollination service was defined as crop yield, whereas metrics of ecological components were widespread throughout. Within each definition, metric choice was not constant. For example, studies defining pollination based on plant fitness used combinations of metrics as diverse as (1) the number of pollinators, pollinator diversity, proportion of nearby uncultivated land, and fruit and seed production (Brittain *et al.* 2010), or (2) number of pollinator visits to each flower and the number of fertile seeds on each flower (Greenleaf and Kremen 2006). Papers defining the service as pollinator abundance/diversity used combinations including (1) pollinator visitation rate (Carvalho *et al.* 2010) and (2) the relative abundance of each species and species richness (Brosi *et al.* 2009). The diversity of measurement approaches – resulting from different ES definitions, components, and metrics – demonstrates that pollination services have not been measured in such a way as to reflect a single, universally comparable benefit for society.

■ Sources of inconsistency

Definitions

The wide range of approaches used to measure pollination services indicates that, even for a single ES, vastly different environmental and social phenomena are being studied. Understanding the major drivers of this measurement-related variability, and knowing whether those drivers can be manipulated, will improve the comparability and capacity for synthesis of ES research. If two studies define the same ES differently, those studies could be measuring different quantities. Defining a specific ES will be influenced by several factors, including the discipline

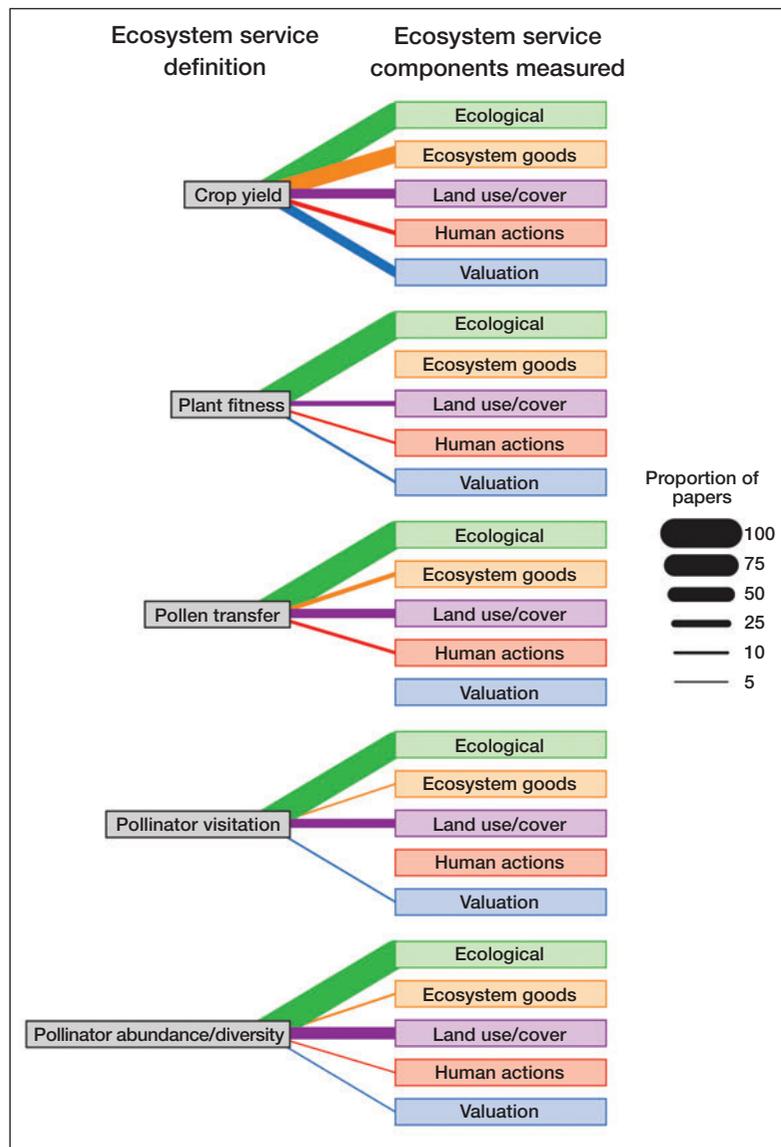


Figure 3. The components (and metrics) used to quantify pollination service provision will change depending on the ES definition used. The width of the lines indicates the proportion of papers using that ES definition and component combination. Note that the proportion of papers measuring valuation and ecosystem good components increases when pollination service is defined as crop yield, while the proportion of papers measuring ecological or land use/cover components remains largely consistent.

of the researchers, their interpretation of ES, and their perspective on human–environment interactions, as well as the objectives of a given study.

Individual disciplines have different measurement traditions and interpret services in the context of those traditions. An ecological economist studying pollination services might focus on social or economic measures, emphasize consumption of pollen-dependent foods, and use definitions related to crop yield (Winfree *et al.* 2011). To quantify the service, that economist might measure how fruit set value increases when pollinators are present (Aizen *et al.* 2009). On the other hand, an ecologist might focus on the biophysical processes at the root of the bene-

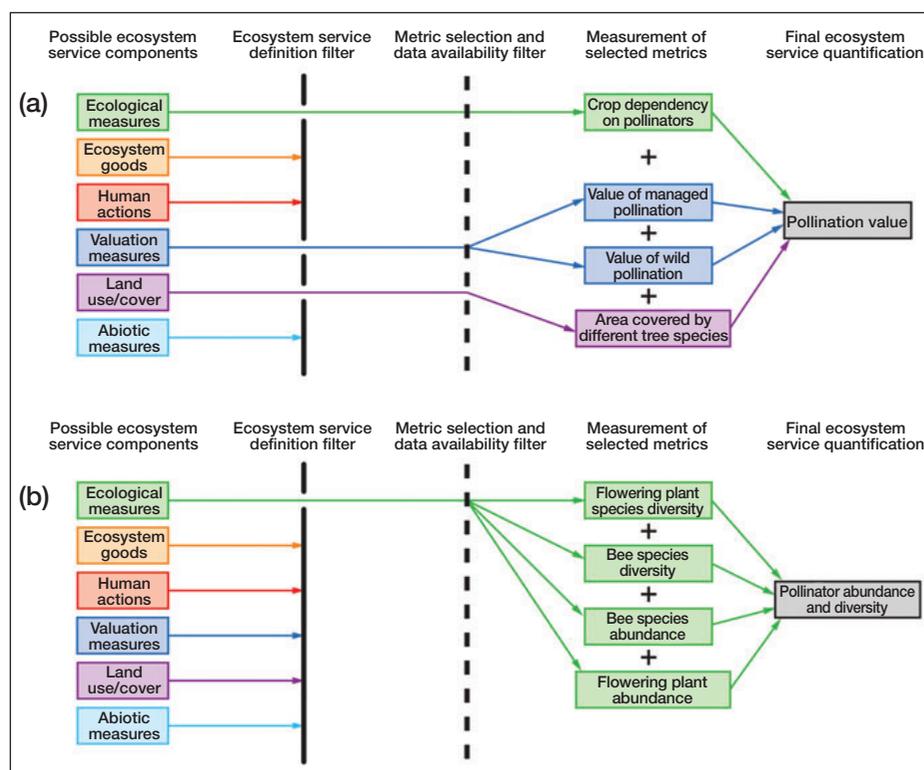


Figure 4. From all possible ES components and metrics, a smaller set is chosen and combined in order to quantify ES provision. The choice will depend on the specific ES definition, the metrics selected to best quantify this definition, and data availability/logistics. Two examples demonstrate how this has led to differences in measuring pollination services. (a) Pollination services are defined as the cost required to completely replace insect pollinators in fruit orchards (Allsopp *et al.* 2008), or (b) pollination services are quantified using the diversity and abundance of pollinator species present in and around almond orchards (Mandelik and Roll 2009). Note that (b) relies only on ecological components and may only capture the biophysical supply of the service rather than actual service delivery.

fit, and identify pollination as pollen transfer. Such a study might quantify the mass of pollen transferred to each flower by pollinators (McKinney and Goodell 2010), and neglect to determine whether this actually increases fruit set or crop yield. Different perspectives on the role of the environment will yield definitions that may or may not include the contribution of human inputs, such as managed honeybees in addition to wild pollinators, in providing pollination services (eg Veddeler *et al.* 2008; Isaacs and Kirk 2010). Each of these approaches can be equally valid, although a measurement limited either to the biophysical capacity of the system to supply the service (eg ecological components) or to the benefit (eg human activity or valuation components) risks failing to capture important aspects of service delivery (Tallis and Polasky 2009; de Groot *et al.* 2010). Further, when researchers engage in interdisciplinary discussions, it is important that they recognize that they may be interpreting the same ES differently.

Answering different ES research questions requires the use of different ES definitions. A study that asks “What are the economic returns from bee pollination in smallholder farming systems?” necessitates a definition related to mar-

ket valuation, such as the value of pollinator-dependent crops (Kasina *et al.* 2009). Alternatively, to answer the question “What contribution do native and non-native pollinators make to pollination services in the study area?”, a definition based on pollinator visitation and diversity is more useful (Winfree *et al.* 2007). Nevertheless, when research objectives are similar, scientists should use the same definition of pollination services to facilitate meaningful inter-study comparison. For example, investigations of human dependence on pollinators are likely distinct from those focusing on the role of land-use planning decisions in maintaining pollination services. A major strength of ES assessment lies in integrating the knowledge from researchers in multiple disciplines (Polasky and Segerson 2009). Using more consistent definitions could allow for new synergies in ES research across disciplines and provide opportunities for synthesis within the ES field. This may require establishing more specific categories of ES, where a larger umbrella term (eg pollination services) is subdivided into several

ES with more narrowly focused definitions.

Component and metric selection

Component selection depends on the concept researchers are trying to capture (ie the ES definition) and the feasibility of using each metric, given the study conditions (UNEP–WCMC 2011). Potential metrics are first limited to those that best represent the components that contribute to service provision. Metric selection further reduces that set to those best suited to the study design and those that are easiest to measure (Figure 4). For a study quantifying the cost of replacing pollinators, this process could involve reducing an initial pool of valuation metrics to only those with data available at a regional scale (eg Allsopp *et al.* 2008). In contrast, a study assessing the role of wild and managed pollinators might narrow an initial set of metrics characterizing biophysical processes to those that describe detailed roles of individual species (eg Mandelik and Roll 2009). These differences can ultimately result in conflicting conclusions about ES provision for the same study area (Panel 1).

The metrics selected to quantify ES often reflect practi-

cal considerations. Data that are accessible may be favored (eg those that are easily collected or already available in existing datasets; UNEP–WCMC 2011; Layke *et al.* 2012). Selected metrics will also reflect measurement conventions within a discipline, often including methods a researcher has experience with. In addition, the temporal or spatial scale of the study may influence which metrics are used and how they are measured. If information is required about how pollination services change at a scale of 75 m, a metric that quantifies the contribution of pollinator-dependent plants to household income will not be useful (Kohler *et al.* 2008). Conversely, for a study of global reliance on pollination services, field observations of pollinator diversity over the

entire study extent will not be feasible (Klein *et al.* 2007).

■ Recommendations

We propose a set of steps to help reduce variability in ES measurement:

- (1) Explicitly define the ES in the context of each study. We found that few studies explicitly defined pollination services. Comparing ES across studies requires clearly identifying what each study intends to quantify.
- (2) Select contextually appropriate ES definitions. Much ES measurement variability stems from the range of definitions currently in use. By using precise and/or

Panel 1. How can findings be affected by ES definitions and metric selection?

Consider two landscapes of equal size, Landscape A and Landscape B. Landscape A consists of a large tract of pollinator-dependent agricultural land, with a small forest patch (Figure 5a). Landscape B consists of a smaller amount of pollinator-dependent agricultural land bordered by a large forest patch, hedgerows, and a meadow (Figure 5b).

The landowner is deciding how to allocate land use between cropland and natural habitat, and is interested in identifying which landscape has greater total pollination services to help inform the decision. Landscape A contains pollinator-nesting habitat of moderate quality, but the cropland extent means that some of the cropland is beyond the pollinator foraging range. This habitat supports a small pollinator population. The pollinator-dependent crop is unevenly pollinated and under-pollinated, and yield per unit area of cropland is low. Landscape B contains extensive pollinator nesting and foraging habitat and supports a larger pollinator population. The entire cropland area is within the pollinator foraging range. The area of the pollinator-dependent crop is limited and is pollen-saturated; increased pollen deposition would not increase crop yield per unit area.

“Pollination services” for each landscape can be measured in many ways, based on the service definition in the study and the metrics selected. The landowner is considering two possible methods:

Method 1: Pollination service is defined as the production of the pollinator-dependent crop from the entire landscape. Two metrics are selected for the measurement: area of cropland (a land-cover component) and crop biomass produced per unit area of cropland (an ecological component). Landscape A has a lower level of production per unit area, but total crop production is higher than in Landscape B, where the high-performing crop covers a limited area.

Method 2: Pollination service is defined as pollinator abundance and diversity. Two metrics are used for this measurement: total number of pollinators observed at the study site, and species diversity of the pollinators. Pollinators are sparse in Landscape A, have low diversity, and do not regularly reach the entire field. In contrast, Landscape B contains several times as many pollinators, and species diversity is higher.

On the basis of Method 1, the landowner concludes that Landscape A has a higher supply of pollination services and would manage the landscape by promoting the area of cropland and biomass produced by the pollinator-dependent crop. Using Method 2, the landowner concludes that the pollination service is greater in Landscape B and takes conservation measures to maintain the diversity of land cover and pollinator habitats. These two simple measurement methods therefore produce contradictory results, based on the assumptions inherent in each definition and the metrics used for quantification.

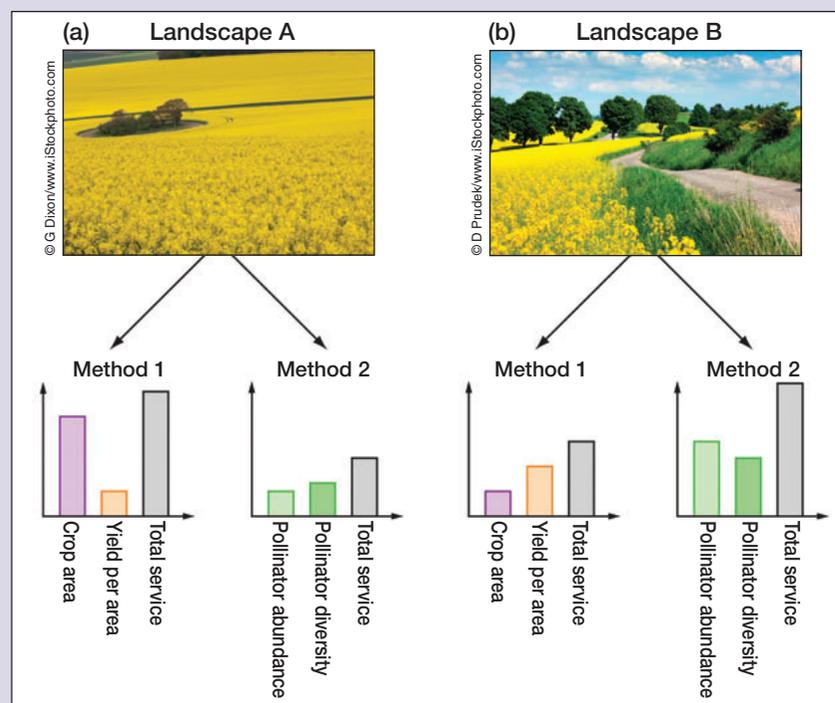


Figure 5. Different ES definitions and metric selections could hypothetically alter study conclusions about pollination service provision and confound comparisons among studies. Pollination services are estimated to be high in Landscape A (a) when using a crop yield definition but low based on pollinator abundance and diversity, while the opposite is true in Landscape B (b). See panel text for a detailed explanation.

consistent definitions, authors would promote more effective comparison of research findings, thereby facilitating synthesis. While ES definitions can and should change based on study objectives, studies asking similar questions should use consistent definitions. This may require expanding the number of types of services, so that each has a specific and narrowly defined meaning.

- (3) Clearly and deliberately choose metrics to measure ES. Researchers need to better recognize the cross-disciplinarity of ES research and the range of metrics that can be used in ES measurement, including ecological, social, and economic variables. Measurement choices should be well reasoned and defensible. Accurate understanding of trends in ES requires appreciating and accounting for the biases that different measurement methods and combinations of metrics introduce.
- (4) Develop tools to guide metric selection for individual services. Although ES definitions will vary across studies, there may be certain components (eg ecological measures, ecosystem goods, valuation measures, land use/cover, abiotic measures) that best represent each definition. Identifying these specific combinations of metrics will increase the potential for comparison among studies. For each individual service, specialists could also establish protocols and tools for use by non-experts, to support consistent metric selection across a variety of scenarios. Broad reviews of metrics and indicators used in ES assessment would provide a useful starting point (UNEP–WCMC 2011; Layke *et al.* 2012).
- (5) Use caution when comparing ES measurements within and among studies. As the number of ES studies increases, there will be increasing comparison among studies to discern the general trends in ES across regions and time. We urge caution when performing these analyses and suggest that consideration of the methods and metrics used to quantify ES among studies should be the first step in these comparisons.
- (6) Ensure management decisions are based on studies using relevant ES measurement techniques. Variability in ES definitions and metrics implies that some studies will not be as directly applicable as others for management and policy. Authors should clearly present the limitations of their analysis and describe the conditions under which the ES definition and metrics they have chosen will be relevant. Researchers and managers should engage with each other to make decisions regarding ES definition and measurement.

■ Conclusions

Using the ES framework to promote conservation and inform environmental policy requires that managers and policy makers fully understand ES research findings,

including their applicability and limitations. Clear, interpretable, and consistently measured results are critical for this purpose. Using pollination services as a case study, we found substantial variation in how a single service is defined and in how the service is measured based on that definition. The results of this analysis reflect patterns that seem to apply to other ES. If management recommendations are made without considering these inconsistencies, it could impede the effective application of the ES framework. To successfully implement ES-informed management strategies, researchers and managers need to understand the implications of study results, and this requires precise knowledge of the quantity assessed and the methods used for measurement. Comparisons of ES trends among studies need to ensure that observed trends in service provision are not confounded by variation in ES measurement.

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■ References

- Aizen MA, Garibaldi LA, Cunningham SA, and Klein AM. 2009. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Ann Bot-London* 103: 1579–88.
- Allsopp MH, de Lange WJ, and Veldtman R. 2008. Valuing insect pollination services with cost of replacement. *PLoS ONE* 3: e3128.
- Ashworth L, Quesada M, Casas A, *et al.* 2009. Pollinator-dependent food production in Mexico. *Biol Conserv* 142: 1050–57.
- Barbier EB. 1994. Valuing environmental functions: tropical wetlands. *Land Econ* 70: 155–173.
- Blanche KR, Hughes M, Ludwig JA, and Cunningham SA. 2006. Do flower-tripping bees enhance yields in peanut varieties grown in north Queensland? *Aust J Exp Agr* 46: 1529–34.
- Bos MM, Veddeler D, Bogdanski AK, *et al.* 2007. Caveats to quantifying ecosystem services: fruit abortion blurs benefits from crop pollination. *Ecol Appl* 17: 1841–49.
- Boyd J and Banzhaf S. 2007. What are ecosystem services? The need for standardized environmental accounting units. *Ecol Econ* 63: 616–26.
- Boyd J and Wainger L. 2003. Measuring ecosystem service benefits: the use of landscape analysis to evaluate environmental trades and compensation. Resources for the Future Discussion Paper 02-63. Washington, DC: Resources for the Future.
- Brittain C, Bommarco R, Vighi M, and Settele J. 2010. Biological conservation – organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biol Conserv* 279: 309–15.
- Brosi BJ, Daily GC, Chamberlain CP, and Mills M. 2009. Detecting changes in habitat-scale bee foraging in a tropical fragmented landscape using stable isotopes. *Forest Ecol Manag* 258: 1846–55.
- Carvalho LG, Seymour CL, Veldtman R, and Nicolson SW. 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *J Appl Ecol* 47: 810–20.
- Chan KMA, Shaw MR, Cameron DR, *et al.* 2006. Conservation planning for ecosystem services. *PLoS Biol* 4: e379.

- Daily GC and Matson PA. 2008. Ecosystem services: from theory to implementation. *P Natl Acad Sci USA* **105**: 9455–56.
- Daily GC, Polasky S, Goldstein J, *et al.* 2009. Ecosystem services in decision making: time to deliver. *Front Ecol Environ* **7**: 21–28.
- Dale VH and Polasky S. 2007. Measures of the effects of agricultural practices on ecosystem services. *Ecol Econ* **64**: 286–96.
- de Groot RS, Alkemade R, Braat L, *et al.* 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecol Complexity* **7**: 260–72.
- Greenleaf SS and Kremen C. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in northern California. *Biol Conserv* **133**: 81–87.
- Hodges KE. 2008. Defining the problem: terminology and progress in ecology. *Front Ecol Environ* **6**: 35–42.
- Isaacs R and Kirk AK. 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *J Appl Ecol* **47**: 841–49.
- Kasina JM, Mburu J, Kraemer M, and Holm-Mueller K. 2009. Economic benefit of crop pollination by bees: a case of Kakamega small-holder farming in western Kenya. *J Econ Entomol* **102**: 467–73.
- Klein A-M, Vaissière BE, Cane JH, *et al.* 2007. Importance of pollinators in changing landscapes for world crops. *P Roy Soc B-Biol Sci* **274**: 303–13.
- Kohler F, Verhulst J, and Van Klink R. 2008. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *J Appl Ecol* **45**: 753–62.
- Lamarque P, Quétiér F, and Lavorel S. 2011. The diversity of the ecosystem services concept and its implications for their assessment and management. *C R Biol* **334**: 441–49.
- Layke C, Mapendembe A, Brown C, *et al.* 2012. Indicators from the global and sub-global Millennium Ecosystem Assessments: an analysis and next steps. *Ecol Indic* **17**: 77–87.
- Lonsdorf E, Kremen C, Ricketts T, *et al.* 2009. Modelling pollination services across agricultural landscapes. *Ann Bot-London* **103**: 1589–600.
- MA (Millennium Ecosystem Assessment). 2005. Ecosystems and human well-being: synthesis. Washington, DC: Island Press.
- Mandelik Y and Roll U. 2009. Diversity patterns of wild bees in almond orchards and their surrounding landscape. *Israel J Plant Sci* **57**: 185–91.
- McKinney AM and Goodell K. 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol Invasions* **12**: 2751–63.
- Nicholson E, Mace GM, Armsworth PR, *et al.* 2009. Priority research areas for ecosystem services in a changing world. *J Appl Ecol* **46**: 1139–44.
- Polasky S and Segerson K. 2009. Integrating ecology and economics in the study of ecosystem services: some lessons learned. *Annu Rev Resour Econ* **1**: 409–34.
- Seppelt R, Dormann CF, Eppink FV, *et al.* 2011. A quantitative review of ecosystem service studies: approaches, shortcomings and the road ahead. *J Appl Ecol* **48**: 630–36.
- Seppelt R, Fath B, Burkhard B, *et al.* 2012. Form follows function? Proposing a blueprint for ecosystem service assessments based on reviews and case studies. *Ecol Indic* **21**: 145–54.
- Tallis H and Polasky S. 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. *Ann NY Acad Sci* **1162**: 265–83.
- Tallis H, Lester SE, Ruckelshaus M, *et al.* 2012. New metrics for managing and sustaining the ocean's bounty. *Mar Policy* **36**: 303–06.
- UNEP–WCMC (United Nations Environment Programme–World Conservation Monitoring Centre). 2011. Developing ecosystem service indicators: experiences and lessons learned from sub-global assessments and other initiatives. Montréal, Canada: Secretariat of the Convention on Biological Diversity. Technical Series No 58.
- Veddeler D, Olschewski R, Tschardt T, and Klein AM. 2008. The contribution of non-managed social bees to coffee production: new economic insights based on farm-scale yield data. *Agroforest Syst* **73**: 109–14.
- Vihervaara P, Rönkä M, and Walls M. 2010. Trends in ecosystem service research: early steps and current drivers. *Ambio* **39**: 314–24.
- Winfree R, Gross BJ, and Kremen C. 2011. Valuing pollination services to agriculture. *Ecol Econ* **71**: 80–88.
- Winfree R, Williams NM, Dushoff J, and Kremen C. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecol Lett* **10**: 1105–13.

■ WebReferences (papers used for case study analysis)

- Adler LS and Hazzard RV. 2009. Comparison of perimeter trap crop varieties: effects on herbivory, pollination, and yield in butternut squash. *Environ Entomol* **38**: 207–15.
- Ahrné K, Bengtsson J, and Elmqvist T. 2009. Bumble bees (*Bombus* spp) along a gradient of increasing urbanization. *PLoS ONE* **4**: e5574.
- Aizen MA, Garibaldi LA, Cunningham SA, and Klein AM. 2009. How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Ann Bot-London* **103**: 1579–88.
- Albrecht M, Duelli P, Müller C, et al. 2007. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *J Appl Ecol* **44**: 813–22.
- Allsopp MH, de Lange WJ, and Veldtman R. 2008. Valuing insect pollination services with cost of replacement. *PLoS ONE* **3**: e3128.
- Amorim ME and De Marco P. 2011. Pollination of *Byrsonima coccolobifolia*: short-distance isolation and possible causes for low fruit production. *Braz J Biol* **71**: 709–17.
- Anderson SH, Kelly D, Ladley JJ, et al. 2011. Cascading effects of bird functional extinction reduce pollination and plant density. *Science* **331**: 1068–71.
- Ashworth L, Quesada M, Casas A, et al. 2009. Pollinator-dependent food production in Mexico. *Biol Conserv* **142**: 1050–57.
- Badano EI and Vergara CH. 2011. Potential negative effects of exotic honey bees on the diversity of native pollinators and yield of highland coffee plantations. *Agric For Entomol* **13**: 365–72.
- Bai Y, Zhuang C, Ouyang Z, et al. 2011. Spatial characteristics between biodiversity and ecosystem services in a human-dominated watershed. *Ecol Complex* **8**: 177–83.
- Balvanera P, Kremen C, and Martínez-Ramos M. 2005. Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecol Appl* **15**: 360–75.
- Barmaz S, Potts SG, and Vighi M. 2010. A novel method for assessing risks to pollinators from plant protection products using honeybees as a model species. *Ecotoxicology* **19**: 1347–59.
- Batary P, Baldi A, Sarospataki M, et al. 2010. Effect of conservation management on bees and insect-pollinated grassland plant communities in three European countries. *Agr Ecosyst Environ* **136**: 35–39.
- Batáry P, Báldi A, Kleijn D, and Tscharntke T. 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *P Roy Soc B-Biol Sci* **278**: 1894–902.
- Bates AJ, Sadler JP, Fairbrass AJ, et al. 2011. Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS ONE* **6**: e23459.
- Blanche KR, Hughes M, Ludwig JA, and Cunningham SA. 2006. Do flower-tripping bees enhance yields in peanut varieties grown in north Queensland? *Aust J Exp Agr* **46**: 1529–34.
- Blanche R and Cunningham SA. 2005. Rain forest provides pollinating beetles for atemoya crops. *J Econ Entomol* **98**: 1193–201.
- Bodin Ö, Tengo M, Norman A, et al. 2006. The value of small size: loss of forest patches and ecological thresholds in southern Madagascar. *Ecol Appl* **16**: 440–51.
- Bommarco R, Lundin O, Smith HG, and Rundlöf M. 2012. Drastic historic shifts in bumble-bee community composition in Sweden. *P Roy Soc B-Biol Sci* **279**: 309–15.
- Bos MM, Veddeler D, Bogdanski AK, et al. 2007. Caveats to quantifying ecosystem services: fruit abortion blurs benefits from crop pollination. *Ecol Appl* **17**: 1841–49.
- Brading P, El-Gabbas A, Zalut S, and Gilbert F. 2010. Biodiversity economics: the value of pollination services to Egypt. *Egypt J Biol* **11**: 46–51.
- Breeze T, Bailey A, Balcombe K, and Potts S. 2011. Pollination services in the UK: how important are honeybees? *Agr Ecosyst Environ* **142**: 137.
- Brittain C, Bommarco R, Vighi M, et al. 2010a. The impact of an insecticide on insect flower visitation and pollination in an agricultural landscape. *Agric For Entomol* **12**: 259–66.
- Brittain C, Bommarco R, Vighi M, et al. 2010b. Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biol Conserv* **143**: 1860–67.
- Brosi BJ, Armsworth PR, and Daily GC. 2008a. Optimal design of agricultural landscapes for pollination services. *Conserv Lett* **1**: 27–36.
- Brosi BJ, Daily GC, Shih TM, et al. 2008b. The effects of forest fragmentation on bee communities in tropical countryside. *J Appl Ecol* **45**: 773–83.
- Brosi BJ, Daily GC, Chamberlain CP, and Mills M. 2009. Detecting changes in habitat-scale bee foraging in a tropical fragmented landscape using stable isotopes. *Forest Ecol Manag* **258**: 1846–55.
- Calle Z, Guariguata M, and Giraldo E. 2010. The production of passion fruit (*Passiflora edulis*) in Colombia: perspectives for habitat conservation through pollination services. *Interciencia* **35**: 207–12.
- Cane JH. 2008. A native ground-nesting bee (*Nomia melanderi*) sustainably managed to pollinate alfalfa across an intensively agricultural landscape. *Apidologie* **39**: 315–23.
- Carvalho LG, Seymour CL, Veldtman R, and Nicolson SW. 2010. Pollination services decline with distance from natural habitat even in biodiversity-rich areas. *J Appl Ecol* **47**: 810–20.
- Carvalho LG, Veldtman R, Shenkute AG, et al. 2011. Natural and within-farmland biodiversity enhances crop productivity. *Ecol Lett* **14**: 251–59.
- Cayenne Engel E and Irwin RE. 2003. Linking pollinator visitation rate and pollen receipt. *Am J Bot* **90**: 1612–18.
- Chacoff NP, Aizen MA, and Aschero V. 2008. Proximity to forest edge does not affect crop production despite pollen limitation. *P Roy Soc B-Biol Sci* **275**: 907–13.
- Chacoff N and Aizen M. 2006. Edge effects on flower-visiting insects in grapefruit plantations bordering premontane subtropical forest. *J Appl Ecol* **43**: 18–27.
- Chan KMA, Shaw MR, Cameron DR, et al. 2006. Conservation planning for ecosystem services. *PLoS Biol* **4**: 2138–52.
- Cook DC, Thomas MB, Cunningham SA, et al. 2007. Predicting the economic impact of an invasive species on an ecosystem service. *Ecol Appl* **17**: 1832–40.
- De Marco P and Coelho FM. 2004. Services performed by the ecosystem: forest remnants influence agricultural cultures' pollination and production. *Biodivers Conserv* **13**: 1245–55.
- Diekötter T, Kadoya T, Peter F, et al. 2010. Oilseed rape crops distort plant-pollinator interactions. *J Appl Ecol* **47**: 209–14.
- Farwig N, Bailey D, Bochud E, et al. 2009. Isolation from forest reduces pollination, seed predation and insect scavenging in Swiss farmland. *Landscape Ecol* **24**: 919–27.
- Fontaine C, Dajoz I, Meriguet J, and Loreau M. 2005. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biol* **4**: e1.
- Forup ML, Henson KSE, Craze PG, and Memmott J. 2008. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *J Appl Ecol* **45**: 742–52.
- Franzen M and Nilsson SG. 2008. How can we preserve and restore species richness of pollinating insects on agricultural land? *Ecography* **31**: 698–708.

Continued

■ WebReferences - continued

- Galen C and Geib JC. 2007. Density-dependent effects of ants on selection for bumble bee pollination in *Polemonium viscosum*. *Ecology* **88**: 1202–09.
- Gallai N, Salles J-M, Settele J, and Vaissière BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecol Econ* **68**: 810–21.
- Gardiner MA, Tuell JK, Isaacs R, *et al.* 2010. Implications of three biofuel crops for beneficial arthropods in agricultural landscapes. *Bioenerg Res* **3**: 6–19.
- Garibaldi LA, Aizen MA, Cunningham SA, and Klein AM. 2009. Pollinator shortage and global crop yield: looking at the whole spectrum of pollinator dependency. *Commun Integr Biol* **2**: 37–39.
- Garibaldi LA, Aizen MA, Klein AM, *et al.* 2011a. Global growth and stability of agricultural yield decrease with pollinator dependence. *P Natl Acad Sci USA* **108**: 5909–14.
- Garibaldi LA, Steffan-Dewenter I, Kremen C, *et al.* 2011b. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol Lett* **14**: 1062–72.
- Gemmill-Herren B and Ochieng AO. 2008. Role of native bees and natural habitats in eggplant (*Solanum melongena*) pollination in Kenya. *Agr Ecosyst Environ* **127**: 31–36.
- Greenleaf SS and Kremen C. 2006a. Wild bee species increase tomato production and respond differently to surrounding land use in northern California. *Biol Conserv* **133**: 81–87.
- Greenleaf SS and Kremen C. 2006b. Wild bees enhance honey bees' pollination of hybrid sunflower. *P Natl Acad Sci USA* **103**: 13890–95.
- Groeneveld JH, Tschamtk T, Moser G, and Clough Y. 2010. Experimental evidence for stronger cacao yield limitation by pollination than by plant resources. *Perspect Plant Ecol* **12**: 183–91.
- Hannon LE and Sisk TD. 2009. Hedgerows in an agri-natural landscape: potential habitat value for native bees. *Biol Conserv* **142**: 2140–54.
- Hegland SJ and Boeke L. 2006. Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecol Entomol* **31**: 532–38.
- Hoehn P, Steffan-Dewenter I, and Tschamtk T. 2010. Relative contribution of agroforestry, rainforest and openland to local and regional bee diversity. *Biodivers Conserv* **19**: 2189–200.
- Hoehn P, Tschamtk T, Tylanakis JM, and Steffan-Dewenter I. 2008. Functional group diversity of bee pollinators increases crop yield. *P Roy Soc B-Biol Sci* **275**: 2283–91.
- Holzschuh A, Steffan-Dewenter I, and Tschamtk T. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *J Anim Ecol* **79**: 491–500.
- Holzschuh A, Steffan-Dewenter I, Kleijn D, and Tschamtk T. 2007. Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *J Appl Ecol* **44**: 41–49.
- Hopwood JL. 2008. The contribution of roadside grassland restorations to native bee conservation. *Biol Conserv* **141**: 2632–40.
- Isaacs R and Kirk AK. 2010. Pollination services provided to small and large highbush blueberry fields by wild and managed bees. *J Appl Ecol* **47**: 841–49.
- Jansson Å and Polasky S. 2010. Quantifying biodiversity for building resilience for food security in urban landscapes: getting down to business. *Ecol Soc* **15**: 20.
- Jauker F, Diekoetter T, Schwarzbach F, and Wolters V. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecol* **24**: 547–55.
- Jha S and Vandermeer J. 2010. Impacts of coffee agroforestry management on tropical bee communities. *Biol Conserv* **143**: 1423–31.
- Julier HE and Roulston TH. 2009. Wild bee abundance and pollination service in cultivated pumpkins: farm management, nesting behavior and landscape effects. *J Econ Entomol* **102**: 563–73.
- Karimzadegan H, Rahmatian M, Salmasi DM, *et al.* 2007. Valuing forests and rangelands-ecosystem services. *Int J Environ Res* **1**: 368–77.
- Kasina JM, Mburu J, Kraemer M, and Holm-Mueller K. 2009. Economic benefit of crop pollination by bees: a case of Kakamega small-holder farming in western Kenya. *J Econ Entomol* **102**: 467–73.
- Keitt TH. 2009. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. *Ecol Appl* **19**: 1561–73.
- Klein A-M. 2009. Nearby rainforest promotes coffee pollination by increasing spatio-temporal stability in bee species richness. *Forest Ecol Manag* **258**: 1838–45.
- Klein A-M, Steffan-Dewenter I, and Tschamtk T. 2006. Rain forest promotes trophic interactions and diversity of trap-nesting Hymenoptera in adjacent agroforestry. *J Anim Ecol* **75**: 315–23.
- Klein A-M, Vaissière BE, Cane JH, *et al.* 2007. Importance of pollinators in changing landscapes for world crops. *P Roy Soc B-Biol Sci* **274**: 303–13.
- Knight ME, Osborne JL, Sanderson RA, *et al.* 2009. Bumblebee nest density and the scale of available forage in arable landscapes. *Insect Conserv Diver* **2**: 116–24.
- Kohler F, Verhulst J, Van Klink R, and Kleijn D. 2008. At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? *J Appl Ecol* **45**: 753–62.
- Kovacs-Hostyanszki A, Batáry P, and Báldi A. 2011. Local and landscape effects on bee communities of Hungarian winter cereal fields. *Agric For Entomol* **13**: 59–66.
- Krauss J, Gallenberger I, and Steffan-Dewenter I. 2011. Decreased functional diversity and biological pest control in conventional compared to organic crop fields. *PLoS ONE* **6**: e19502.
- Kremen C, Williams NM, and Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. *P Natl Acad Sci USA* **99**: 16812–16.
- Kremen C, Williams N, Bugg R, *et al.* 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol Lett* **7**: 1109–19.
- Kühn I, Bierman SM, Durka W, and Klotz S. 2006. Relating geographical variation in pollination types to environmental and spatial factors using novel statistical methods. *New Phytol* **172**: 127–39.
- Lautenbach S, Kugel C, Lausch A, and Seppelt R. 2011. Analysis of historic changes in regional ecosystem service provisioning using land use data. *Ecol Indic* **11**: 676–87.
- Lonsdorf E, Kremen C, Ricketts T, *et al.* 2009. Modelling pollination services across agricultural landscapes. *Ann Bot-London* **103**: 1589–600.
- Losey J and Vaughan M. 2006. The economic value of ecological services provided by insects. *BioScience* **56**: 311–23.
- Mandelik Y and Roll U. 2009. Diversity patterns of wild bees in almond orchards and their surrounding landscape. *Isr J Plant Sci* **57**: 185–91.
- McKinney AM and Goodell K. 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol Invasions* **12**: 2751–63.
- Medan D, Pablo Torretta J, Hodara K, *et al.* 2011. Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina. *Biodivers Conserv* **20**: 3077–100.

Continued

■ WebReferences - continued

- Memmott J, Waser NM, and Price MV. 2004. Tolerance of pollination networks to species extinctions. *P Roy Soc B-Biol Sci* **271**: 2605–11.
- Morandin LA and Winston ML. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agr Ecosyst Environ* **116**: 289–92.
- Morandin LA, Winston ML, Abbott VA, and Franklin MT. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? *Basic Appl Ecol* **8**: 117–24.
- Olschewski R, Klein A-M, and Tschardt T. 2010. Economic trade-offs between carbon sequestration, timber production, and crop pollination in tropical forested landscapes. *Ecol Complex* **7**: 314–19.
- Olschewski R, Tschardt T, Benitez PC, *et al.* 2006. Economic evaluation of pollination services comparing coffee landscapes in Ecuador and Indonesia. *Ecol Soc* **11**: 7.
- Olschewski R, Tschardt T, Benitez P, *et al.* 2007. Economic evaluation of ecosystem services as a basis for stabilizing rainforest margins? The example of pollination services and pest management in coffee landscapes. In: Tschardt T, Leuschner C, Zeller M, *et al.* (Eds). *Stability of tropical rainforest margins: linking ecological, economic and social constraints of land use and conservation*. Berlin, Germany: Springer-Verlag.
- Otieno M, Woodcock BA, Wilby A, *et al.* 2011. Local management and landscape drivers of pollination and biological control services in a Kenyan agro-ecosystem. *Biol Conserv* **144**: 2424–31.
- Perfectti F, Gómez JM, and Bosch J. 2009. The functional consequences of diversity in plant–pollinator interactions. *Oikos* **118**: 1430–40.
- Petrosillo I, Zaccarelli N, and Zurlini G. 2010. Multi-scale vulnerability of natural capital in a panarchy of social–ecological landscapes. *Ecol Complex* **7**: 359–67.
- Philpott S, Uno S, and Maldonado J. 2006. The importance of ants and high-shade management to coffee pollination and fruit weight in Chiapas, Mexico. *Biodivers Conserv* **15**: 487–501.
- Plieninger T, Schleyer C, Mantel M, and Hostert P. 2011. Is there a forest transition outside forests? Trajectories of farm trees and effects on ecosystem services in an agricultural landscape in eastern Germany. *Land Use Policy* **29**: 233–43.
- Potts SG, Petanidou T, Roberts S, *et al.* 2006. Plant–pollinator biodiversity and pollination services in a complex Mediterranean landscape. *Biol Conserv* **129**: 519–29.
- Potts SG, Vulliamy B, Dafni A, *et al.* 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* **84**: 2628–42.
- Presley SJ, Willig MR, Saldanha LN, *et al.* 2009. Reduced-impact logging has little effect on temporal activity of frugivorous bats (Chiroptera) in lowland Amazonia. *Biotropica* **41**: 369–78.
- Priess JA, Mimler M, Klein AM, *et al.* 2007. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. *Ecol Appl* **17**: 407–17.
- Pywell RF, Meek WR, Loxton RG, *et al.* 2011. Ecological restoration on farmland can drive beneficial functional responses in plant and invertebrate communities. *Agr Ecosyst Environ* **140**: 62–67.
- Ricketts T. 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conserv Biol* **18**: 1262–71.
- Ricketts TH, Daily GC, Ehrlich PR, and Michener CD. 2004. Economic value of tropical forest to coffee production. *P Natl Acad Sci USA* **101**: 12579–82.
- Ricketts TH, Regetz J, Steffan-Dewenter I, *et al.* 2008. Landscape effects on crop pollination services: are there general patterns? *Ecol Lett* **11**: 499–515.
- Samnegard U, Persson AS, and Smith HG. 2011. Gardens benefit bees and enhance pollination in intensively managed farmland. *Biol Conserv* **144**: 2602–06.
- Sargent RD, Kembel SW, Emery NC, *et al.* 2011. Effect of local community phylogenetic structure on pollen limitation in an obligately insect-pollinated plant. *Am J Bot* **98**: 283–89.
- Satake A, Rudel TK, and Onuma A. 2008. Scale mismatches and their ecological and economic effects on landscapes: a spatially explicit model. *Global Environ Chang* **18**: 768–75.
- Schulpe CJE and Alkemade R. 2011. Consequences of uncertainty in global-scale land cover maps for mapping ecosystem functions: an analysis of pollination efficiency. *Remote Sensing* **3**: 2057–75.
- Sobek S, Tschardt T, Scherber C, *et al.* 2009. Canopy vs. understory: does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecol Manag* **258**: 609–15.
- Taki H, Okabe K, Makino S, *et al.* 2009. Contribution of small insects to pollination of common buckwheat, a distylous crop. *Ann Appl Biol* **155**: 121–29.
- Taki H, Okabe K, Yamaura Y, *et al.* 2010. Effects of landscape metrics on *Apis* and non-*Apis* pollinators and seed set in common buckwheat. *Basic Appl Ecol* **11**: 594–602.
- Tylianakis JM, Tschardt T, and Lewis OT. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**: 202–05.
- Underwood T, McCullum-Gomez C, Harmon A, and Roberts S. 2011. Organic agriculture supports biodiversity and sustainable food production. *J Hunger Environ Nutr* **6**: 398–423.
- Veddeler D, Olschewski R, Tschardt T, and Klein AM. 2008. The contribution of non-managed social bees to coffee production: new economic insights based on farm-scale yield data. *Agroforest Syst* **73**: 109–14.
- Watson JC, Wolf AT, and Ascher JS. 2011. Forested landscapes promote richness and abundance of native bees (Hymenoptera: Apoidea: Anthophila) in Wisconsin apple orchards. *Environ Entomol* **40**: 621–32.
- Westphal C, Steffan-Dewenter I, and Tschardt T. 2009. Mass flowering oilseed rape improves early colony growth but not sexual reproduction of bumblebees. *J Appl Ecol* **46**: 187–93.
- Williams NM and Kremen C. 2007. Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecol Appl* **17**: 910–21.
- Wilson J, Messinger O, and Griswold T. 2009. Variation between bee communities on a sand dune complex in the Great Basin Desert, North America: implications for sand dune conservation. *J Arid Environ* **73**: 666–71.
- Winfree R and Kremen C. 2008. Are ecosystem services stabilized by differences among species? A test using crop pollination. *P Roy Soc B-Biol Sci* **276**: 229–37.
- Winfree R, Aguilar R, Vázquez DP, *et al.* 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* **90**: 2068–76.
- Winfree R, Gross BJ, and Kremen C. 2011. Valuing pollination services to agriculture. *Ecol Econ* **71**: 80–88.
- Winfree R, Williams NM, Dushoff J, and Kremen C. 2007. Native bees provide insurance against ongoing honey bee losses. *Ecol Lett* **10**: 1105–13.
- Winfree R, Williams NM, Gaines H, *et al.* 2008. Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *J Appl Ecol* **45**: 793–802.