# Population diversity and ecosystem services

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**The current rate of biodiversity loss threatens to disrupt greatly the functioning of ecosystems, with potentially significant consequences for humanity. The magnitude of the loss is generally measured with the use of species extinction rates, an approach that understates the severity of the problem and masks some of its most important consequences. Here, we propose a major expansion of this focus to include population diversity: considering changes in the size, number, distribution and genetic composition of populations and the implications of those changes for the functioning of ecosystems and the provision of ecosystem services. We also outline the key components of population diversity and describe a new approach to delineating a population unit that explicitly links it to the services that it provides**

Species loss dramatically represents the mass extinction currently underway [1–4]. Yet, species extinctions are an inadequate measure of biodiversity loss and do not provide information about changes in the capacity of particular species to contribute to the functioning of ecosystems. Balmford *et al.* (this issue) provide persuasive arguments for focusing on changes in population size and habitat extent when measuring the state of nature. We also emphasize that the relationship between biodiversity and human well being is primarily a function of populations of species. Whether the benefits of biodiversity are conveyed directly (e.g. food) or indirectly (e.g. pollination), their supply is generally determined by the diversity of populations producing them [5]. Hence, population change can have a substantial impact on an ecosystem that is independent of changes in species diversity.

The consequences of population loss for species conservation are well recognized, but have been little addressed from the viewpoint of the functioning of ecosystems and the provision of ecosystem services [6–9]. Recent research has begun to explore the link between species populations and the services that they provide [10–12], even to the point where species-specific services have been identified [13]. Here, we argue that this approach should be greatly expanded for two reasons: (1) to assess the theoretical and practical implications of population change for the functioning of humanity's life-support systems; and (2) to reflect more accurately the state of global biodiversity.

Population change can occur through variation in the number of populations for a given species, the number of individuals per population, the spatial distribution of populations, and the genetic differentiation within and among populations. Historically, the term 'population diversity' has largely been used by geneticists when discussing genetic differentiation (e.g., [14–16]), or as a measure of the number of Mendelian populations in a given area [6]. These approaches are limited because they ignore important demographic characteristics of populations that can influence the provision of ecosystem services. We argue that assessments of population diversity should consider both the demographic (e.g. size, number and distribution) and genetic nature of populations.

Here, we have two aims: (1) to develop a new population unit categorization that explicitly links a population with the ecosystem service(s) that it provides; and (2) to provide an extended definition of population diversity that formalizes its most important dimensions in an ecosystem context. We present a conceptual framework for exploring the relationships between population diversity and the functioning of ecosystems. Investigating these relationships empirically in even a few systems presents major challenges, but we hope our discussion stimulates debate and innovative ideas about empirical investigations of what we believe is an area of crucial importance. The terms 'ecosystem service' and 'ecosystem function' are largely interchangeable, as used here, although ecosystem services can be defined as ecological processes that benefit people [9], whereas ecosystem functions can be considered as all ecological processes regardless of whether they are beneficial to humanity.

## Defining population units and the importance of population change

There are many approaches to defining species populations [17–22]. Consistently problematic is defining population boundaries so that the number of populations can be clearly determined [6]. Geneticists use measures of gene flow and genetic differentiation to distinguish one population from another [23]. In a demographic sense, this can be achieved by careful measures of individual movement (e.g. [24]), which enables the delineation of populations that are sufficiently isolated from each other to have independent dynamics [25] (Box 1). Populations can also be distinguished with the use of some arbitrarily

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defined spatial and/or temporal context (e.g. linear distance between groups, or the presence of geographical barriers or other spatial disjunctions) or differences in phenology, morphology or physiology.

The above distinctions are important from the perspective of species conservation, but they might be inadequate when assessing the contribution that a group of individuals from a given species makes to an ecosystem service. To address this issue, we suggest that it is essential to recognize the link between a group of individuals and the ecosystem service(s) that it provides, and use this as a further criterion to delineate populations. We refer to this new population categorization as a 'service-providing unit' (SPU; Boxes 1,2).

Imagine a single species occupying a heterogeneous environment such that groups of individuals can be distinguished on the basis of habitat suitability or the spatial characteristics of the landscape (e.g. a rainforest-dependent species occupying forest fragments in an agricultural landscape). The groups might be linked by sufficient dispersal to classify them as belonging to a single evolutionary unit (EU) or demographic unit (DU; Box 1). However, each group provides nonoverlapping, localized services to areas of the surrounding landscape, suggesting that they could be categorized as different SPUs. For example, Kremen *et al.* [12] demonstrate that pollination services provided by native bee populations to watermelon crops are reduced on farms that are distant from native

## Box 1. Taxonomy of populations

### Evolutionary unit

Evolutionary units (EUs) are populations with independent evolutionary dynamics. Thus, a classic Mendelian population (a reproductive community of sexual and cross-fertilizing individuals which share a common gene pool) [40] is an EU. Using neutral loci will generally circumscribe larger EUs than would using loci under strong, geographically varying selection. An example of EUs is the island populations of various plant species (from the Family Asteraceae) that evolved different diaspore morphology and reduced dispersal ability, compared with the mainland populations from which they originated [41].

### Demographic unit

Demographic units (DUs) are populations with independent demographic dynamics. In general, populations that fluctuate in size asynchronously, or are shown to have only a few (or no) migrants pass between them, should be considered DUs. A classic example of a set of DUs is the now-extinct three populations of the checkerspot butterfly *Euphydryas editha* in the Jasper Ridge Biological Reserve of Stanford University. They had asynchronous dynamics [42,43] and delineating the DUs was crucial to understanding those dynamics. Local populations in metapopulations are ordinarily DUs, but DUs are not necessarily elements of metapopulations.

### Conservation unit

The designation of conservation units (CUs) will depend on the associated conservation goals, which vary tremendously. Goals oriented around evolution typically involve maintaining the genetic diversity of a species, or the potential for future genetic divergence or speciation. Pursuit of these goals has been formalized using concepts such as minimum viable populations [44–46], evolutionarily significant units [47–49], and so-called management units [48]. Here, we focus on the goal of maintaining ecological functions and their associated ecosystem services.

### Service-providing unit (SPU)

The new population category that we propose is a service-providing unit (SPU). SPUs provide, or might provide in the future, a recognized ecosystem service at some temporal or spatial scale. All populations are potentially SPUs and the population categories described here can overlap (e.g. a single population might be an EU, DU, CU and SPU). This will not always be the case, making it crucial to delineate SPUs when assessing the consequences of population change for the provision of ecosystem services. For example, population categories might occur in a nested hierarchy (Fig. Ia) and the loss of a SPU might not result in the loss of a DU or CU, but still might have consequences for the functioning of local ecosystems. Alternatively, multiple DUs, CUs or EUs might comprise a single SPU (Fig. Ib). For example, multiple DUs of a plant species might provide a water purification service to a given area and loss of a few DUs might not adversely disrupt the provision of the service (Box 2).

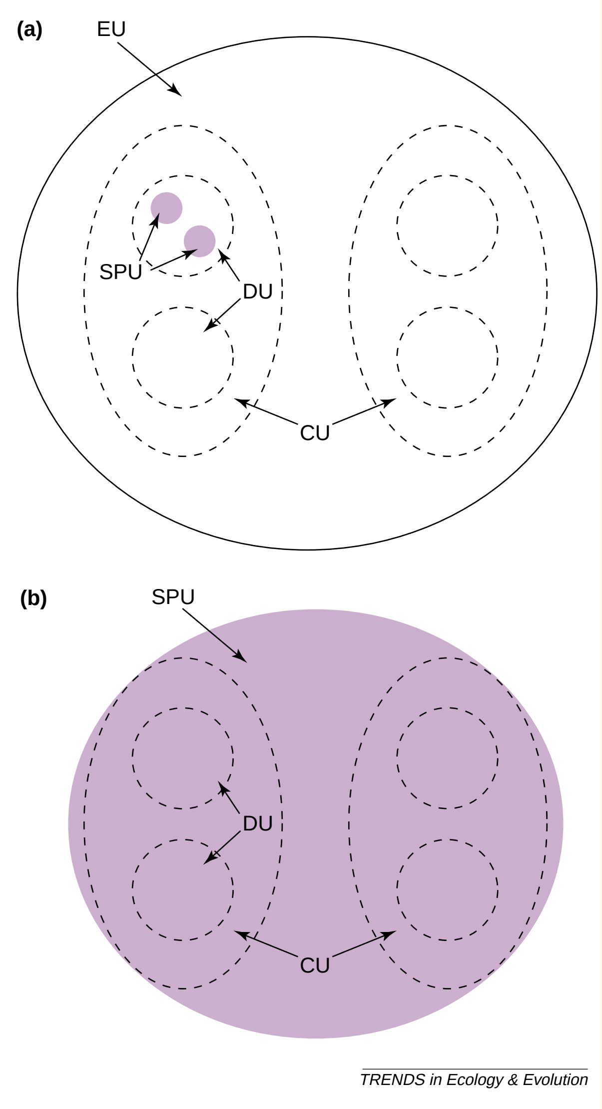

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**Fig. I.**

**Box 2. What is a service-providing unit?**

The delineation of a service-providing unit (SPU) will vary depending on the ecosystem service being considered, and any temporal or spatial variation inherent in the species of interest and the service itself. For example, the entire population of a given tree species might provide the global service of carbon sequestration. Regional populations of the same tree species might provide a water filtration service that benefits local communities (whereas populations in other regions might not). Very localized populations might provide livestock protection for individual farms. Another example is generalist pollinators that might be frequent visitors to particular plant species only during certain seasonal conditions, such as when other flowering resources are scarce, or certain pollinator populations that are only important to crops during crucial flowering periods. Service provision and the delineation of SPUs can occur at multiple levels and will probably depend as much on our social institutions (e.g. what they acknowledge as a service and the geographical scope of their operation [50]), as they do on scientific issues.

vegetation ($<1\%$ of natural habitat within a 1-km radius), which provides nesting and foraging resources for the bees. In agricultural landscapes with scattered patches of native vegetation that support bee populations (equivalent to a collection of individuals in this context), the distance between patches (and, hence, populations) appears to be crucial to the provision of pollination services. In the example above, distances $>2$ km between populations would mean that pollination services are nonoverlapping. In cases such as these, populations should be considered SPUs because the loss of particular populations (e.g. through native habitat clearance) has implications for service provision. Moreover, it is realistic to suggest that multiple, spatially discrete SPUs can comprise a single EU, DU or conservation unit (CU), and just focusing on the loss of these latter categories as a measure of population decline might not adequately assess the consequences of population change for the provision of pollination services.

This example raises two important issues. First, the consequences of the loss of a SPU (of a single species) will be dependent, in part, on the capacity of individuals from neighboring extant SPUs (of the same species) to cover the loss (e.g. through re-colonization of habitat, assuming that habitat clearance is not the cause of the loss). The extinction and colonization dynamics of networks of localized populations are the focus of the burgeoning research on metapopulation theory (e.g. [26]). Under some circumstances, a SPU might be analogous to a local population in a metapopulation context if there is sufficient movement among SPUs. The important issue is the time taken to recolonize a site and to reinstate a given service, and the time constraints associated with that service. In the example given above, even short-term (e.g. <six months) loss of bee populations can have significant consequences for pollination success if it occurs during a crucial period (e.g. crop flowering), and can impact greatly on farm productivity in a given year.

The second important issue is the number of species that contribute to a service and the capacity of extant species to compensate for the loss of a SPU of any given species. It is most likely that multiple species contribute to a particular service, although the extent of this contribution seems to vary among species and services [12,13,27]. This issue is related to the controversial topic of ecological redundancy [28–30]. If multiple species contribute to the same ecosystem service(s), it is possible that the loss of one or more SPUs of a given species might not result in severe ecosystem disruption if extant SPUs are able to compensate for the loss. Redundancy is clearly an important ecosystem characteristic, because having multiple species contributing to the same service(s) provides some insurance against ecosystem disruption if the populations of a particular species are lost [29,31,32].

Considering the potential for functional similarity among species, a complementary approach to that outlined here could be to designate within- or cross-taxon functional guilds (comprising multiple species populations that contribute to the same function) as SPUs. One can then assess changes in functional guild diversity (e.g. richness of functional guilds, number of individuals and species across guilds, and spatial distribution) and the potential consequences for the functioning of ecosystems and the provision of services. However, the probable variation among species in the contribution that they make to a particular service means that putting them all into a single guild might mask important species-level differences. Moreover, all species contribute to the functioning of ecosystems, and changes in population diversity will have implications at some level (e.g. reduced ecosystem reliability or resilience). Variability in the contributions of species to ecosystem services suggests that different single-species SPUs might have different ‘service-providing value’ and the range of these values should be an important focus for future research.

## Key components of population diversity

There are four key components of population diversity: richness, the size of each population, spatial distribution and differentiation.

### *Population richness*

Population richness is the number of populations of a species in a given area, which depends on the criteria used to delineate population boundaries. When the focus is on ecosystem services, we propose using as a criterion the spatial disjunctions in the services provided by conspecific individuals occupying a heterogeneous environment (i.e. SPUs). If the required data are unavailable, standard genetic or demographic approaches would be the next best option.

### *Population size*

Data about the number of individuals per population provide an indication of the frequency distribution of population sizes. Absolute numbers would be the most useful, but, owing to the difficulty of obtaining such information, orders of magnitude or some other representative measure might be more appropriate. It is important to document the distribution of population sizes to determine whether a species is characterized by, for example, a single large population and many small populations, or several similarly sized populations. This distribution has implications, not only for species conservation, but also for the contribution that each population makes to the functioning of ecosystems, and raises the important issue of how variability in the number of individuals in a given population affects functionality. Our approach is most applicable when there are clear spatial disjunctions among groups of individuals, although population discreteness is best measured using the genetic, demographic or ecosystem service approaches we describe here. For ubiquitous species for which discrete populations cannot be identified, variability in population density might be a useful surrogate.

Kearns *et al.* [27] provide examples in which pollination services are disrupted when the population size falls below a certain level. Moreover, they also show how changes in population density (for plants or pollinators) can alter pollination success. For example, they cite the study of Roll *et al.* [33], which found that seed production in *Lesquerella fendleri* was greater for plants with a high density of conspecifics, possibly as a consequence of the behavior of the associated pollinators. Soulé *et al.* [34] discuss, in detail, a concept that they refer to as ‘ecologically effective population densities’, for which dramatic changes in the densities of interactive species (e.g. predators and their prey) can have substantial consequences for the functioning of ecosystems. Hence, not only is the number of individuals in each population important, but it also appears that the number of individuals in a given area requires careful consideration. A SPU can become ‘functionally extinct’ at very low densities or abundance.

### Population distribution

The third component of population diversity is the spatial distribution of the populations under study. The important measures here are the extent of the populations relative to their maximum possible extent in a defined area, and population dispersion. Focusing on maximum possible extent facilitates comparisons between species with large geographical ranges and those with relatively restricted ranges. Geographical range is a measure of the maximum area in which a species can provide a given service. An assessment of population extent might consider, for example, the number of sites that populations occupy relative to all possible sites available for occupancy. This would be applicable in landscapes in which populations are tied to spatially discrete habitat patches and it is relatively easy to identify suitable, but currently unoccupied patches. If data are available, the current extent of populations could also be compared with the historic geographical range of the target species (e.g. before a major perturbation, such as the European colonization of Australia) [7].

Population dispersion is a measure of the spatial aggregation of populations and how this can affect the delivery of services over a given area. For example, the services provided by fish populations might be extremely localized owing to natural (e.g. shorelines) or anthropogenic boundaries (e.g. regional fisheries) and the adaptation of populations to a narrow range of environmental variability [10]. Deep-rooted tree species, which can control water-table levels and thus reduce the adverse effects of dryland salinity in agricultural regions of southern Australia, might be most effective in controlling salinization if dispersed among various recharge areas (where the water table is replenished), rather than clustered in a single area or only among discharge areas (where the water table rises to the surface) [35].

### Genetic differentiation of populations

The final component of population diversity is genetic differentiation within and among populations. From both conservation and ecosystem service perspectives, more genetic variation within populations might confer greater resilience in the face of environmental change (such as the possible stabilizing influence of genetic diversity in key

### Box 3. Practical application

The practical application of our approach is challenging, but we believe substantial progress can be made with carefully designed studies. Two important areas require empirical investigation: (1) linking populations of species to the ecosystem service(s) that they provide; and (2) assessing the consequences of population change for service provision.

Studies on the former are well under way [11–13]. Researchers could approach this by taking a given service in a particular context (e.g. pest control in an orchard) and investigating which species contribute to this service, or taking a single species and determining which of various services it contributes to. Although challenging, both approaches appear tractable in at least a local context (e.g. a single farm). Most problematic is assessing changes in populations and how these affect service provision. One approach for animals that have specific habitat requirements might be to link populations to habitat patches and use changes in the extent or quality of habitat as a surrogate for changes in populations (similar to the species–area relationships used to estimate species extinction rates). This would initially require careful study of the relationships between the population characteristics of a given species and its habitat, but once these are established, researchers could develop rules-of-thumb for population–habitat dynamics, which means that the demographic characteristics of each population need not be studied directly. A similar patch-based approach could be applied to populations of plant species, where change in habitat (equals vegetation communities in many instances) extent could be measured over large areas using aerial photographs or remotely sensed imagery. For example, researchers could examine changes over time in the characteristics of patches of deep-rooted trees and what consequences this might have had for the occurrence of dryland salinity. Regardless of the method used to estimate population change, researchers should investigate whether the change corresponds with variability in the delivery of a given service. For example, does clearance of a habitat patch coincide with reduced pollination success in an adjacent crop? Detailed studies that link population change with variation in the delivery of ecosystem services would help to develop predictions of the probable outcome of changes in poorly studied systems. These predictions could be tested by focusing just on changes in the delivery of services, without the need to assess population change directly. However, there are limits to inferring quantitative population change from measures of variability in service delivery only, because this variability might be the result of changes in species behaviour. We advocate the establishment of model landscapes where these issues can be explored in depth [51]. Results from such studies will help guide direction for future research and focus attention on the services provided by nature that are indispensable to our continued existence.

tree species enabling forests to track climate change; e.g [36]). Genetic differentiation among populations can be associated with different types or levels of a given ecosystem service. For instance, some grass populations (e.g. *Agrostis tenuis*) have evolved genetic characteristics that enable them to colonize mine tailings and other sites with soil mineral concentrations that are lethal to other populations of the same species [37], giving them value as soil stabilizers. Perhaps the most important ecosystem service in which study of genetic differentiation of populations is crucial is in maintaining or augmenting crop yields, which depends on genetic material that often is only available from populations of wild relatives of crops [38,39].

## Population change and biodiversity decline

We raise two crucial issues in this article. First, focusing on changes in population diversity is a more comprehensive assessment of biodiversity decline than is a narrow emphasis on the loss of species alone. Rough estimates of large-scale population loss have already been attempted [5,6]. We argue that consideration of population size, distribution, genetic differentiation and density are also needed to reflect accurately the consequences of population change. This focus requires a meaningful definition of 'population'. We argue here that measuring changes in populations defined by certain genetic or demographic criteria, although a useful first step, might not adequately account for the consequences of population change for the functioning of ecosystems and the provision of ecosystem services to humanity. Hence, the second crucial issue we raise is the value of tying groups of individuals to the services that they provide and using this to define a new population category (SPUs).

We do not suggest that traditional species-based approaches should be abandoned when assessing biodiversity decline, but argue that the consequences of changes in population diversity merit much more attention than they currently receive. A comprehensive measure of biodiversity loss should include both species- and population-based approaches. We believe that categorizing groups of individuals from the same species into SPUs, and focusing on changes in SPU diversity, is a meaningful population-based approach, and one that is tractable in many crucial economic situations (e.g. crop pollination) (Box 3). Reduced diversity has implications for species conservation and the contribution that a particular species can make to the provision of ecosystem services. Adequate population diversity provides insurance against change in environmental conditions and confers greater flexibility on ecological communities for coping with anthropogenic or nonanthropogenic stress.

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