Trends in Ecology & Evolution

Opinion

Evosystem Services: Rapid Evolution and the Provision of Ecosystem Services

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Evolution is recognized as the source of all organisms, and hence many ecosystem services. However, the role that contemporary evolution might play in maintaining and enhancing specific ecosystem services has largely been overlooked. Recent advances at the interface of ecology and evolution have demonstrated how contemporary evolution can shape ecological communities and ecosystem functions. We propose a definition and quantitative criteria to study how rapid evolution affects ecosystem services (here termed contemporary evosystem services) and present plausible scenarios where such services might exist. We advocate for the direct measurement of contemporary evosystem services to improve understanding of how changing environments will alter resource availability and human well-being, and highlight the potential utility of managing rapid evolution for future ecosystem services.

Eco- and Evo-system Services

Ecosystem services (see Glossary) are properties or processes of ecosystems that confer direct or indirect benefits to humans [1]. With increasing human impacts on the biosphere, there is tremendous concern about the provisioning of ecosystem services in the future [2]. Previous work has highlighted that many conservation goals can be met only with the assistance of adapting taxa [3,4], yet the relationship between evolution and ecosystem services remains mostly unexplored. **Contemporary evolution** has been documented in many species and several empirical studies have demonstrated that evolution can occur on timescales short enough to alter ecological dynamics [5–10]. If evolution acts quickly enough to shape ecological processes, it is also rapid enough to change, and perhaps even enhance, ecosystem services. Although there are a growing number of studies that have directly measured the contribution of contemporary evolution of dominant species on associated communities and ecosystems [10], none has attempted to connect these ecological changes to their effects on ecosystem services. Here we argue that an understanding of the frequency and relative importance of the process of **rapid evolution** in the provisioning of ecosystem services is a critical part of understanding and managing these services in the future.

Ecosystem services link the functioning of ecosystems and the material or nonmaterial benefits that humans derive from them [1,11]. The concept of ecosystem services has proved its utility by identifying that there are economic benefits that humanity obtains from specific ecosystem functions [12] and by bringing additional political and economic weight to conservation goals [13]. In addition, the concept extends beyond monetization to locate, quantify, and formalize nonmaterial ways that people relate to nature, such as education through food gathering and place-based history [14,15].

Trends

Evolutionary change can occur rapidly enough to alter community dynamics and ecosystem functions.

Despite evidence of the importance of rapid evolution in ecological processes, there has been little discussion of the role of rapid evolution in the provisioning of ecosystem services.

We discuss putative cases where rapid evolution could alter the provision of ecosystem services, which we define as contemporary evosystem services, with a focus on cases where evolution enhances or maintains services.

We provide criteria for measuring these contemporary evosystem services with the aim of spurring empirical research on the link between rapid evolution and ecosystem services.

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Previous discussions of connections between evolution and ecosystem services have focused on the fact that evolution generates biodiversity over the long term [16]. While the mechanistic links between biodiversity and ecosystem services are complex and have recently received more empirical attention [17,18], the links between evolutionary processes themselves and ecosystem services have not received similar detailed attention. There have been calls for a more explicit accounting for the role of evolution in ecosystem services [10,19], including the creation of the term **evosystem services**: 'all the uses or services to humans that are produced from the evolutionary process' [20]. The focus of this term is to give credit to evolution for providing the foundation for all ecosystem services, with the intent that recognizing this connection might help to mitigate against the trend towards seeing all of nature as appropriate fodder for specific management and fine-tuning [21]. However, given that all living organisms, and hence a part of all ecosystem services, stem from evolution this definition counts all ecosystem services as evosystem services, a concept too meta-scale to measure (Figure 1, green). To explicitly address the potential importance of contemporary evolution to the provisioning of ecosystem services we define **contemporary evosystem services** as the maintenance or increase of an ecosystem service resulting from evolution occurring quickly enough to alter ecological processes (Figure 1, dotted line). Here we discuss the evidence for, and the potentially important role of, contemporary evosystem services.

To date, much attention has focused on the negative health and economic impacts that evolution can cause. These ecosystem dis-services can result from contemporary evolution in species that pose costs, such as antibiotic-resistant microbes or insecticide-resistant crop pests [19,22,23]. Reductions to ecosystem services could also stem from the evolution of beneficial species, as selection could lead to **phenotypic** shifts that reduce the provisioning of associated ecosystem services. However, given that intraspecific variation can have profound positive effects on ecosystem services [24] and that selection on intraspecific variation is common in nature [25], evolution is almost certainly enhancing ecosystem services in some cases. The fact that no study has formally observed a contemporary evosystem service likely stems from the fact that none have tested for them. Here we detail the evidence for contemporary evosystem services and highlight the mechanisms by which evolution might provide these services in two broad categories: directional selection and gene flow. We also discuss how to assess the relative importance of contemporary evosystem services (Box 1) and investigate ways to manage them. Ultimately, we hope to further integrate evolution and conservation biology by formalizing the overall contribution of rapid evolution to the provision of ecosystem services.

Contemporary Evosystem Services from Directional Selection

Pollution, climate change, and invasive species can all cause reduced biodiversity and sometimes erode ecosystem services [13]. These stressors can also act as agents of directional selection and drive evolutionary change [26,27]. Research in **eco-evolutionary dynamics** has demonstrated that directional selection can cause contemporary evolution in key species that then shapes communities and ecosystem functions [8,28]. Similarly, adaptation in response to directional selection might enhance or maintain ecosystem services when these services depend on the abundance or presence of a key species affected by a stressor (Figure 2). In some cases directional selection leading to adaptation can even rescue populations or species from extinction. We outline specific case studies that are likely to lead to directional selection that enhances or maintains ecosystem services.

Pollution and Contemporary Evosystem Services

Pollution is a costly consequence of modern human activity [11]. For example, eutrophication in freshwater, where excessive nitrogen and phosphorous can cause blooms of toxic cyanobacteria, leads to damage estimated at US$2.2 billion annually in the USA alone [29]. Cyanobacteria blooms, which few aquatic grazers can efficiently consume, can lead to decreases in

Glossary

Character displacement: the evolution of enhanced functional trait differences between populations or species when they occur in sympatry owing to competition.

Contemporary evolution: trait evolution observed over less than a few hundred generations.

Contemporary evosystem services: the maintenance or increase of an ecosystem service resulting from evolution that occurs quickly enough to alter ecological processes; a subset of evosystem services occurring in contemporary time periods.

Eco-evolutionary dynamics: cases where rapid evolution directly alters population dynamics, ecological communities, or ecosystems.

Ecosystem services: the properties and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life.

Evosystem services: 'all the uses or services to humans that are produced from the evolutionary process' [20]; includes both historical and contemporary evolution, large and small scales, and fast and slow processes.

Phenotypic evolution: heritable change in phenotype frequencies due to genetic changes across generations.

Rapid evolution: a genetic change occurring rapidly enough to have a measurable impact on simultaneous ecological change.

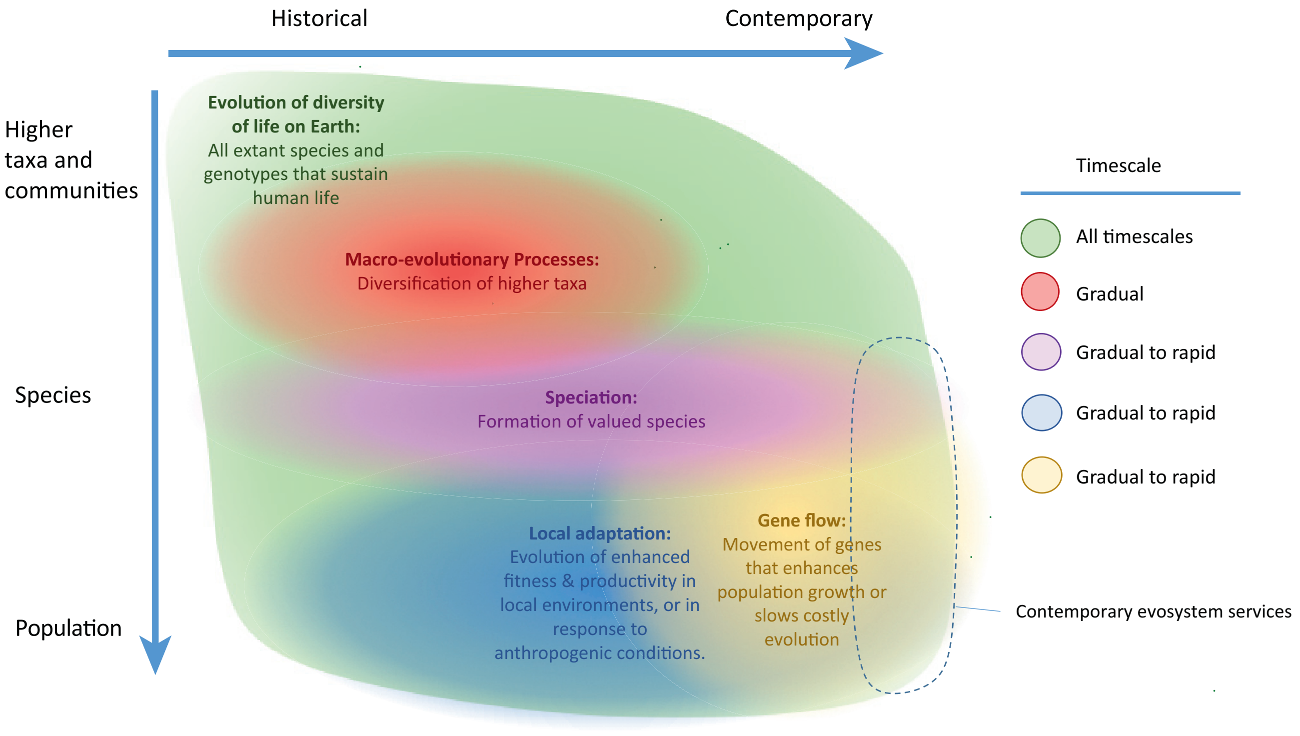

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Figure 1. Conceptual Framework for Evosystem Services and Constituent Processes. Clouds represent the most common locations for each process along the axes but are not exhaustive. Text below each process denotes the way the process could contribute to evosystem services. All of the evolutionary processes that have led to life on Earth (green) have produced a 'storehouse and factory' for all ecosystem services, including as-yet unknown future services. Nested within, the macroevolutionary processes of adaptive radiation (red) and speciation (purple) have produced clade- and species-level biodiversity and resulting services. Local adaptation of populations (blue) has contributed to valuable diversity at a localized scale historically and in present-day scenarios. Gene flow between populations or species provides genetic diversity and can accelerate or slow the pace of evolution, sometimes in ways that enhance ecosystem services. The focus of this Opinion article is rapid evolution (dotted area) through the processes of speciation, local adaptation, and gene flow. These processes cause trait change (often in response to anthropogenic changes) that can alter the provisioning of ecosystem services.

oxygen and, ultimately, fish kills [30]. However, some species of *Daphnia*, a widespread genus of zooplankton, are able to adapt rapidly to feeding on these toxic algae, potentially reducing the costs associated with eutrophication and thereby providing a contemporary evosystem service [31–33].

Box 1. Measuring Contemporary Evosystem Services

To demonstrate a contemporary evosystem service, it is necessary to document contemporary evolution and the resulting phenotypic changes that increase ecosystem-derived benefits to humans. A test therefore requires a 'no-evolution' control to serve as a comparison of the benefits that would be available had evolution not occurred. To quantify the value of an ecosystem service requires estimation of the units of service gained as a consequence of evolution. For example, *Daphnia* is a particularly promising system for an attempt at an initial test of the role of evolution in providing ecosystem services because of the accessibility of 'pre-evolution' genotypes (through resting eggs) to serve as controls and because it is a keystone species in many aquatic food webs [82]. Use of such controls in *Daphnia* has helped to establish that rapid evolution occurred in response to eutrophication of lakes near human population centers (Figure I).

In cases where directional selection does not lead to a contemporary evosystem service, gene flow could still provide benefits to humans by slowing the pace of undesirable evolution or by reducing inbreeding depression. In these cases gene flow prevents what otherwise would have been a loss of ecosystem services due to evolution. Measuring contemporary evosystem services derived from gene flow would entail a comparison between a no-gene-flow control and a gene flow treatment. Farmed areas with and without pesticide refuges could be tractable for these types of comparisons as farms with refuges would be likely to have a slower rate of costly pesticide resistance evolution in pest species due to gene flow from neighboring refuges. Observational work could be useful in documenting the benefits of gene flow in systems where experiments are unwieldy. For example, fish in marine protected areas are not subject to selection from human harvesting. The harvesting of fish can cause populations to evolve in ways that reduce the benefits obtained [83,84]. Documenting gradients in genotypes and/or phenotypes associated with gene flow from protected areas into areas of harvest would suggest a contemporary evosystem service.

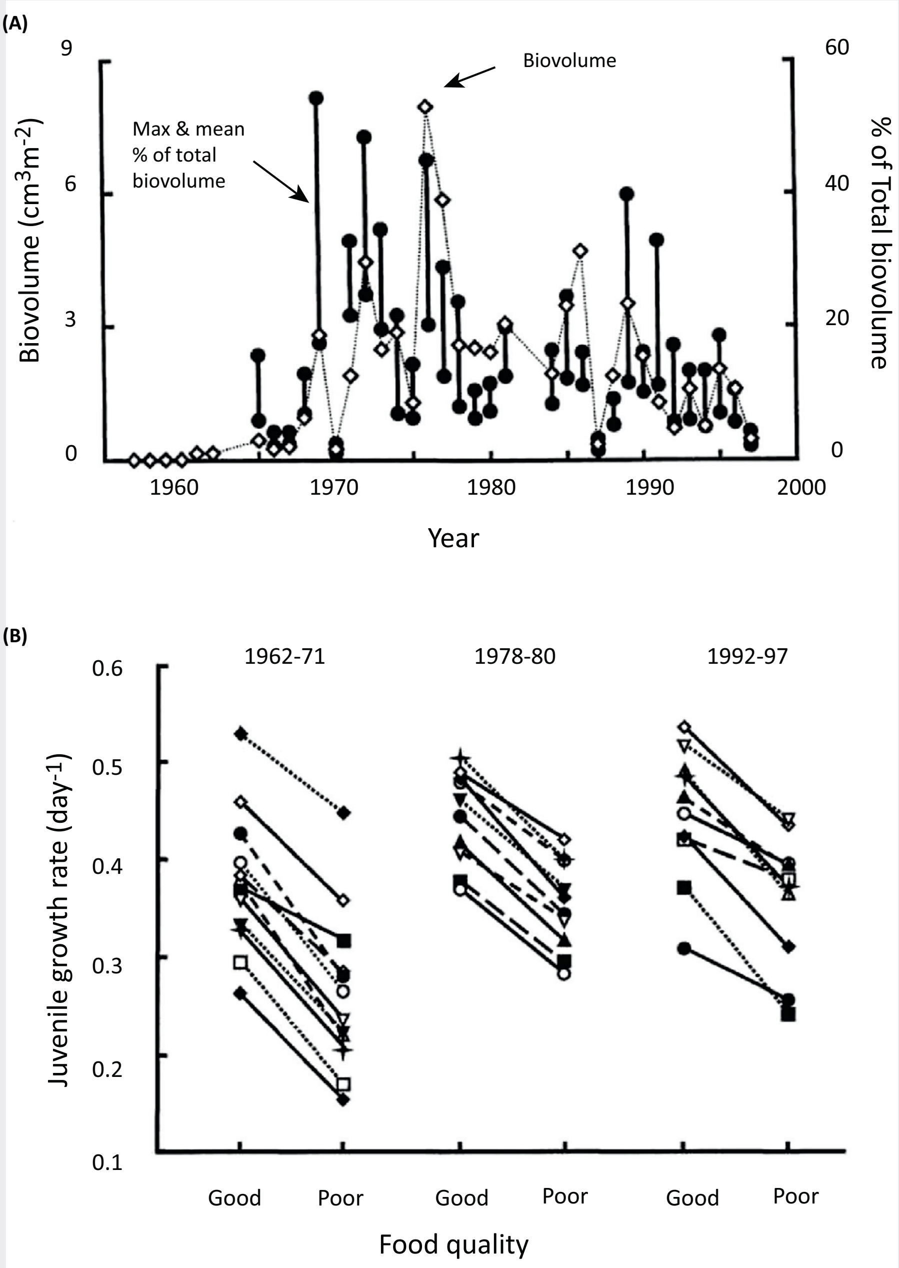

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Figure I. *Daphnia* Show Evolution in Response to Pollution That Is Suggestive of a Contemporary Evosystem Service. Eutrophication occurred in Lake Constance between 1973 and 1993, during which time concentrations of toxic cyanobacteria reached high levels seasonally as shown by the increase of cyanobacteria in the phytoplankton biovolume (A). *Daphnia* from Lake Constance evolved during this time, leading to higher growth rates on microcystin-containing cyanobacteria. This is shown by the greater growth rates on poor diets and the reduced slopes between 'Good' and 'Poor' in the later time period (B). Reproduced from [32].

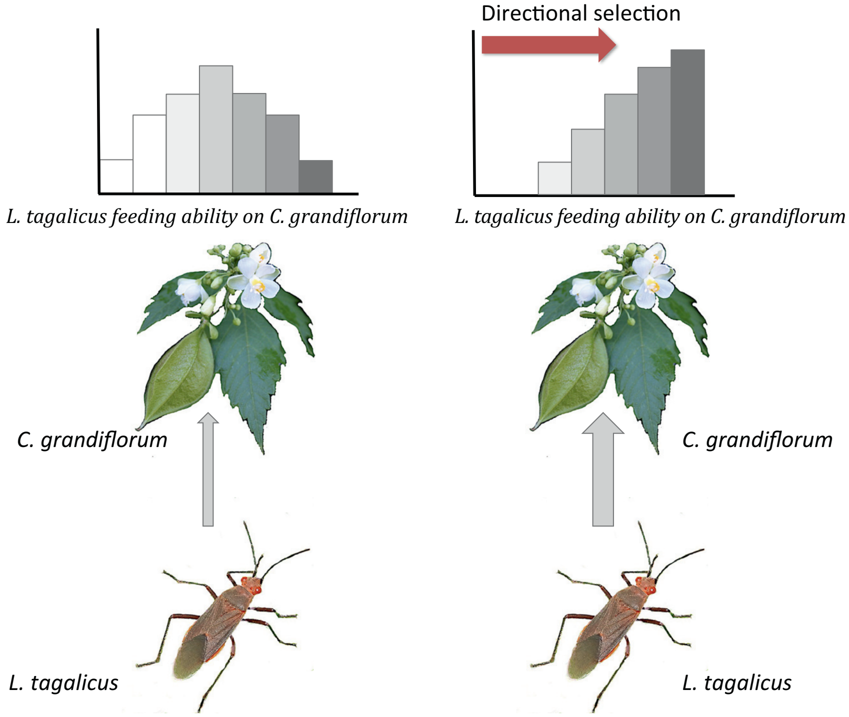

Figure 2. A Hypothetical Contemporary Evosystem Service from Directional Selection. Hypothetical frequency distributions of heritable phenotypes before and after directional natural selection on standing genetic variation. Shading of bars corresponds to the amount of ecosystem service provided by each herbivore phenotype. This illustrated example shows how directional selection on a trait, in this case beak length and feeding ability of *Leptocoris tagalicus* on the invasive plant *Cardiospermum grandiflorum* [57,58], could lead to an evosystem service by reducing the damage associated with *C. grandiflorum* invasion. Thickness of arrows corresponds to the strength of the feeding interaction of *L. tagalicus* on *C. grandiflorum*.

A dramatic illustration of this occurred in Lake Constance, which experienced a period of eutrophication that caused an increase in microcystin toxin-containing cyanobacteria. Adaptation by cyanobacteria-eating *Daphnia galeata* was demonstrated by reviving dormant resting eggs from lake sediment across a span of decades. *D. galeata* raised from eggs obtained before the eutrophication event showed a low growth rate when fed a diet containing cyanobacteria. However, *D. galeata* reared from eggs obtained after eutrophication showed a higher rate of growth on the same diet, demonstrating adaptation to eutrophic conditions (see Figure I in Box 1). It is likely that this event was not unique. *Daphnia pulicaria* shows widespread local adaptation to toxic algae in high-phosphate lakes [33] and experimental work has documented that *Daphnia pulex* rapidly evolved to feeding on cyanobacteria [26]. Such evolution not only benefits the zooplankton; some *Daphnia* clones feed so effectively on cyanobacteria, they can suppress cyanobacterial blooms [34].

There are other cases where contemporary evolution in a species that is not itself economically important could help remediate pollution, thereby helping to restore ecosystem services that are a function of a broader community. For example, the evolution of metal tolerance in soil-stabilizing plants [35] and evolution in marine organisms to cope with ocean acidification [36]. In addition, microbial communities have been shown to respond rapidly to various pollutants, from metals to explosives [37,38]. Toxin-tolerant microbial species can have substantial economic value as part of cost-effective bioremediation [39] and hence the evolution of new tolerant species might represent an important evosystem service. Evolution in response to point-source pollution might currently be providing widespread contemporary evosystem services, but these remain to be measured.

Climate Change and Contemporary Evosystem Services

As average global temperatures continue to climb due to increases in greenhouse gasses [40], adaptation to higher temperatures will be crucial in maintaining many ecosystem services [41,42]. Several studies have provided evidence that phenotypes have shifted in concert with warming temperatures but few have tested whether these shifts are beneficial, heritable, and driven by rising temperatures [43,44]. No study has sought to demonstrate that climate-driven evolution maintains ecosystem services, but there are suggestive cases. For instance, several salmonid species exhibit changes in both physiology [45] and phenology in association with warming temperatures [46], leading to reduced extinction risk [47] and potentially maintaining valuable salmon runs. In a second putative example, field studies have found that soil microbes downregulate their respiration in response to warming, thereby attenuating the expected loss of soil carbon in a warming climate [48]. The contribution of evolution to these changes has not been empirically measured (and there are certainly other mechanisms involved; Box 2), but soil microbes are ripe for experimentation and likely to have sizeable climate impacts. Overall, warming temperatures are likely to lead to evolution that maintains ecosystem services, but conclusive examples or quantitative measures are lacking.

Contemporary Evosystem Services from Evolutionary Rescue

Evolutionary rescue occurs when a population in decline experiences a heritable shift in phenotype that restores positive population growth. Thus, evolutionary rescue has the potential to provide tremendous contemporary evosystem services, as any services from the rescued population would be due, in part, to the process of rapid evolution. evidence for evolutionary rescue in natural systems is scant [49,50]. Links between theoretical and laboratory-based studies (several of which have documented the importance of evolutionary rescue) and field empirical studies are needed to create an understanding of both how often and when evolution will rescue natural populations [51]. Without more evidence from natural populations, it is impossible to estimate the importance of this process to ecosystem services.

Invasive Species and Contemporary Evosystem Services

The establishment of invasive species is typically associated with declines in native species and major environmental damage costing US$120 billion per year [52]. The number of antagonistic interactions that invasive species face can shape the probability of invasion success [53] and

Box 2. Plasticity and Eco- and Evosystem Services

Trait change is the mechanism by which rapid evolution can alter ecological processes [85] and potentially lead to evosystem services. Trait change can be the result of genetic changes, as is the focus of much of this Opinion article, or of plasticity. Plasticity, the ability of one genotype to produce different phenotypes in response to different environments, has long been considered a potential source of resilience that could maintain ecosystem services in the face of rapidly changing environments and extinction [86]. In the same way that trait change stemming from evolution could alter ecosystem services, trait change from phenotypic plasticity could also impact ecosystem services. Plastic changes are not usually heritable and therefore these effects are unlikely to provide long-lasting change to ecosystems or the services they provide, particularly if environmental conditions change.

The relationship between plasticity and contemporary evolution has received intense focus and there are ways that plasticity could alter contemporary evosystem services. The ability of an organism to plastically alter its phenotype in response to differing environments is itself a genetically based trait that could be modified by selection. The increase in *Daphnia galeata* growth rates when feeding on a cyanobacteria-containing diet following a period of eutrophication was due to the evolution of increased phenotypic plasticity (see Figure I in Box 1) [32]. Maladaptive plasticity, where plastic trait shifts reduce organismal fitness, can lead to strong selection and rapid evolution that counteracts plasticity [87]. If maladaptive plasticity had negatively affected an ecosystem service, this would increase the likelihood, and the effect, of a contemporary evosystem service.

constrain the abundance of invasive species [54]. Invasives interact with native species as novel hosts, predators, competitors, or parasites and can act as agents of selection that drive rapid evolution of native species [55]. Therefore, it is possible that rapid evolution helps to reduce the losses associated with invasive species. For example, adaptation in native species that enhances performance during antagonistic interactions with invasives could reduce the abundance of invasive species. Alternatively, **character displacement** in response to invasive species could reduce competition, maintaining ecosystem services by allowing coexistence between invasive species and beneficial native species. Invasive species themselves could also evolve in ways that reduce associated costs (e.g., evolution of reduced virulence in emergent diseases [56]). To date no quantitative work has been undertaken to determine whether contemporary evolution following invasion provides a contemporary evosystem service, but there are several suggestive cases.

In one such case, *Leptocoris tagalicus*, a native Australian bug, evolved a longer beak after the establishment of the invasive balloon vine (*Cardiospermum grandiflorum*). Balloon vine is a destructive invasive in Australia that can smother other plants, including threatened rainforest [57,58]. A feeding experiment demonstrated that *L. tagalicus* individuals with a longer beak were able to feed more effectively on balloon vine [57] (Figure 2). Another putative example involves *Rhagoletis pomonella*, a fruit fly that has specialized on agricultural apples leading to crop losses of 30–70% without pesticides. To mitigate pest transmission, exporters of apples are required to cold-treat apples, which adds costs of 20–30% [59]. However, several parasitoids that feed on *R. pomonella* have evolved specialist races that now feed on the agriculturally damaging host races of *Rhagoletis* [60,61], potentially leading to a reduction of *Rhagoletis* populations and associated costs. Quantitative experimental work is needed to assess the value of the contemporary evosystem services provided in the above cases and to study potential services stemming from antagonistic interactions between native and invasive species in general. Experiments could investigate how adapted and naïve populations of native species affect the growth rates or fitness of invaders and whether rapid evolution might mitigate the loss of ecosystem services often associated with invasion.

Evolutionary mechanisms that reduce competition between invasive species and economically important native species (character displacement) could also represent a contemporary evosystem service. Following the invasion of alewife (*Alosa pseudoharengus*, a zooplanktivorous fish) in Lake Michigan, several native species that primarily consumed zooplankton declined or went locally extinct, including six of seven native lake whitefish species [62]. The bloater chub (*Coregonus hoyi*), the remaining native whitefish, underwent a documented shift in habitat and morphology that led to reduced competition with the invasive alewife, likely due to the evolutionary process of character displacement [62]. This reduced competition might have allowed coexistence, preventing complete extinction of the endemic radiation of deepwater whitefish in Lake Michigan [63]. Alewife and bloater chub are important forage fish for adult lake trout (*Salvelinus namaycush*) [63], a fish with considerable economic and intrinsic value [64]. Systems in which multiple fish species have been stocked in the same watershed or have come into secondary contact following dam removal could be used to investigate how character displacement might reduce competition and whether it leads to increases in the biomass of species of benefit to humans.

Although invasive species are damaging to ecosystems and associated services, there are other cases where introduced species provide a considerable boost to ecosystem services. Valuable salmonid fisheries based on introduced taxa provide numerous examples of the ecosystem services an introduced species can provide (e.g., Great Lakes, Argentina, Chile, New Zealand). In these cases contemporary evolution to local conditions would constitute an evosystem service. For example, introduced Chinook salmon exhibit local adaptation to two

New Zealand streams 26 generations after introduction [65]. Given that recently introduced populations could be distant from local fitness optimums, it seems likely that these populations will exhibit rapid evolution, which in some cases could lead to contemporary evosystem services [65,66].

Contemporary Evosystem Services Resulting from Gene Flow

There are many scenarios in which directional selection, often caused by human harvest or management, would lead to an evolved decline in ecosystem services. In some of these cases, gene flow can provide evosystem services by slowing the pace of evolution in species for which rapid evolution would otherwise lead to a loss of services. In other cases gene flow can facilitate adaptation and evosystem services by introducing genetic diversity that counteracts inbreeding depression, increasing adaptive potential, or facilitates the spread of beneficial genetic variants [67]. Overall, the effect of gene flow on contemporary evosystem services would be shaped by whether the species in question has a positive or negative effect on ecosystem services, whether gene flow facilitates or stymies adaptation, and the effect that local adaptation has on the provisioning of ecosystem services. Below we outline specific cases whereby gene flow would be likely to produce a contemporary evosystem service.

Gene Flow Slowing the Pace of Evolution of Species That Have Negative Effects on Services

Gene flow can provide contemporary evosystem services by slowing the pace of unwanted adaptation in pest species. For example, several recent models have predicted that the presence of wild salmon populations in proximity to ocean-cage-farmed salmon can prevent or slow the evolution of insecticide resistance in farm-infesting sea lice [68,69]. Gene flow from insecticide-susceptible sea lice on wild salmon swamps the spread of insecticide-resistant alleles on salmon farms, delaying or preventing resistance and thereby providing an evosystem service (M. Kreitzman *et al.*, unpublished). A similar process is likely in land-based agriculture, where gene flow from pesticide-free refuges near farms that employ pesticides counteracts the evolution of pesticide resistance. These refuges dilute the effects of directional selection for resistance because they provide areas lacking directional selection favoring resistance. Thus, refuges can lower resistance allele frequency and the probability that resistance reaches fixation [70]. Refuge scenarios provide a tractable opportunity to empirically measure the value of the evosystem services stemming from the mitigation of undesirable directional selection through gene flow. Experiments manipulating the amount of gene flow from refuges and tracking the associated benefits would be highly informative. Species that produce egg banks or dormant seeds that allow gene flow from past populations could also be particularly useful for the assessment of evosystem services (or disservices) emerging from gene flow that slows evolution.

Gene Flow Facilitating Adaptation and Contemporary Evosystem Services

In addition to the mitigation of selection detrimental to ecosystem services, gene flow can lead to increased population growth rates, potentially leading to population- or species-level rescue and the recovery of associated ecosystem services. Genetic rescue, sometimes considered a subcase of evolutionary rescue, is the process whereby gene flow to small populations experiencing inbreeding depression can provide an infusion of new alleles that dilutes deleterious homozygous alleles characteristic of inbreeding, increasing population growth [71]. Genetic rescue has been successfully employed in several charismatic species with cultural value, from bighorn sheep [72] to European vipers [73] and Florida panthers [74]. Similarly, gene flow can facilitate adaptation in natural populations. For example, long-distance dispersal in forest trees allows sharing of genetic variation among populations that are locally adapted to different regimes [75]. This sharing of genetic diversity, in concert with strong directional

Table 1. Evidence for Putative Evosystem Services

Evolutionary process	Mechanism of evosystem service supply	Evosystem service benefit (E, established; P, putative)	Rapid phenotypic shift	Documented heritable	Feasible to manage	Refs
Adaptation	Local adaptation of salmonid populations in >30 generations in New Zealand	E: higher abundance of locally valuable fish	X	X	X	[66]
	Improved growth of *Daphnia* when consuming cyanobacteria	E: reduced costs associated with eutrophication	X	X	X	[26, 31–33]
	Increased copper tolerance in a grass (*Agrostis tenuis*)	P: favorable conditions for further colonization and remediation	X	X		[35]
	Improved growth of coccolithophore (*Emiliania huxleyi*) when experiencing acidified conditions	P: favorable conditions for further colonization and remediation	X	X		[36]
	Microbial community change in response to pollutants	E: remediation of polluted environments	X		X	[39]
	Intraspecific variation in Chinook salmon thermal tolerance	E: higher abundance of Chinook salmon			X	[45]
	Shifts in timing of salmonid spawning runs	E: abundance of salmonids	X		X	[46,47]
	Downregulation of soil microbe metabolism at warm temperatures	E: climate regulation through carbon storage	X			[48]
	Increased benthic foraging of bloater chub (*Coregonus hoyi*) reducing competition with alewife	P: higher abundance of trout	X			[62]
	Longer beak length of *Leptocoris tagalicus* following invasion of balloon vine	P: reduced balloon vine invasiveness	X	X		[57,58]
Speciation	Specialization of *Diachasma alloeum* to feed on *Rhagoletis pomonella*	E: reduced crop losses due to apple maggot	X	X		[60]
Gene flow	Slowing of insecticide-resistance evolution	E: reduced losses in salmon farms	X	X	X	[68,69]

Table 1. (continued)

Evolutionary process	Mechanism of evosystem service supply	Evosystem service benefit (E, established; P, putative)	Rapid phenotypic shift	Documented heritable	Feasible to manage	Refs
	in parasitic marine copepods					
	Slowing of insect resistance to Bt crops	E: reduced pesticide costs	X	X	X	[70]
	Genetic rescue of bighorn sheep (*Ovis canadensis*)	E: increase of a culturally important species	X	X	X	[72]
	Genetic rescue of European viper (*Vipera berus*)	E: increase of a culturally important species	X	X	X	[73]
	Genetic rescue of Florida panther (*Puma concolor*)	E: increase of a culturally important species	X	X	X	[74]
	Slowing of selection pressure from fishing	E: slowing of negative effects of overfishing			X	[77]

We describe examples from the literature based on three evolutionary processes (column 1). Columns 2 and 3 describe the mechanism of supply and the benefit derived from each putative example of an evosystem service. Benefits derived are distinguished by E, for established and documented benefits, and P, for putative benefits that are logical but not documented. Columns 4 and 5 denote whether the pace of phenotypic change is rapid and whether the phenotypic change is heritable. Column 6 is our assessment of the practicality of managing for the enhancement of evosystem services in each putative case through habitat conservation, controlling gene flow, or population translocations.

selection, has been predicted to facilitate evolutionary responses fast enough to allow persistence under predicted climate shifts, even in long-lived tree species [76].

Evolutionary Refuges and Managing for Evosystem Services

Managing for evosystem services would require an integrative view of conservation management that takes into account the selective landscape, intraspecific genetic diversity (or adaptive potential), ecosystem services provision, and the benefit derived from the services. From a practical perspective, manipulating gene flow would be one of the simpler interventional ways to manage for evosystem services (for the practicality of management scenarios, see Table 1). In some scenarios the value of gene flow from relatively unperturbed environments could be great enough to warrant the establishment of 'evolutionary refuges'. These areas could protect genetic diversity and facilitate gene flow [77], particularly in cases where humans exert strong selection through harvesting or agriculture. For example, models suggest that marine protected areas (in which no fishing occurs) might mitigate the evolutionary effects of size-selective harvesting on target species [78], which can otherwise push fish towards smaller sizes. Gene flow in these cases would act counter to fisheries-driven selection outside protected areas, potentially leading to increases in mean fish size but decreases in mean fitness. Thus, the relative contribution to ecosystem services would depend on whether the increase in mean size outweighed the cost of decreased fitness. This example demonstrates that managing for contemporary evosystem services should also entail accounting for the potential negative effects of rapid evolution. In other cases, such as gene flow in pest species from pesticide-free refuges near farms, the benefits of gene flow, and hence management for contemporary evosystem services, would be more straightforward [79].

The homogenizing effect of a large amount of gene flow could be detrimental in cases where directional selection leads to adaptation that generates the ecosystem services (Box 1). In these cases restricting gene flow would be likely to maximize the benefits from adaptation [3]. These vastly different prescriptions for effective evolutionary conservation make it crucial to understand the local adaptation and contemporary evolution of populations to optimize management. In practice, obtaining the necessary information to make these decisions would be challenging. A population that is exhibiting rapid evolution might have a negative population growth rate (i.e., mean absolute fitness <1), but this alone does not necessarily indicate that adaptation is occurring quickly enough to ultimately yield positive population growth. Information about the absolute fitness of particular genotypes, the strength of local adaptation, the role of particular genotypes in provisioning ecosystem services, and population demographics would all be needed. More work on the genetics of adaptation within a metapopulation framework coupled with demographic studies and their effect on evosystem services would help to illuminate general patterns to guide conservation.

Concluding Remarks

The economic costs of rapid evolution in cases of antibiotic and pesticide resistance have been highly publicized. Contemporary evolution in these scenarios has justifiably received much attention in applied evolutionary biology [80] because it counters efforts to remove unwanted species. In many management scenarios, humans exert considerable directional selection so evolution is likely to produce costs or reduce ecosystem services. A growing number of studies have now demonstrated that rapid evolution can alter ecological communities and ecosystem processes [10], sometimes even in cases where the rapid evolution is cryptic [81]. As detailed above, in some cases this rapid evolution is almost certainly contributing to human well-being. Developing a basic understanding of when this occurs and how great the benefits are is a first step towards using this evolution to manage for future ecosystem services. Here we have outlined the motivation for documenting contemporary evosystem services, provided a definition, and highlighted the most promising examples (noting where they fall short of satisfying the criteria) with the goal of spurring research to understand the relationship between rapid evolution and species of cultural and economic importance. Ecologists and conservation biologists might in turn integrate these relationships in the development of strategies to conserve biodiversity and optimize the provision of ecosystem services.

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