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Evolution in the Anthropocene: Informing Governance and Policy

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Abstract

The Anthropocene biosphere constitutes an unprecedented phase in the evolution of life on Earth with one species, humans, exerting extensive control. The increasing intensity of anthropogenic forces in the twenty-first century has widespread implications for attempts to govern both human-dominated ecosystems and the last remaining wild ecosystems. Here, we review how evolutionary biology can inform governance and policies in the Anthropocene, focusing on five governance challenges that span biodiversity, environmental management, food and other biomass production, and human health. The five challenges are: (*a*) evolutionary feedbacks, (*b*) maintaining resilience, (*c*) alleviating constraints, (*d*) coevolutionary disruption, and (*e*) biotechnology. Strategies for governing these dynamics will themselves have to be coevolutionary, as eco-evolutionary and social dynamics change in response to each other.

1. INTRODUCTION

Anthropocene: the term denotes the period in the history of the Earth characterized by human domination of the Earth's processes

Anthromes: classification of the Earth's terrestrial surface according to type and degree of human interaction with ecosystems

Governance: decision-making and power-sharing across all levels of society

Supplemental Material >

Humans dominate evolutionary dynamics on planet Earth (Carroll et al. 2014, Palumbi 2001). The size of the human population and the scale, connectivity, and speed of human actions are major forces in the Anthropocene biosphere (Folke et al. 2016), shaping evolution through anthropogenic environmental change (Hendry 2016). Further, at the turn of the twenty-first century, humans are increasingly in direct control of the evolution of species across the Earth (Bar-On et al. 2018). Using the concept of anthromes (Ellis et al. 2010), we can divide the degree of direct human evolutionary control into three types of evolutionary anthromes (**Figure 1**; **Supplemental Table 1**), in which humans (*a*) artificially select the dominant species covering the surface of the Earth, (*b*) select and to varying degrees control the reproduction of large grazing animals, and (*c*) influence evolution through varying levels of harvest pressure and selection. On land, humans control the propagation of dominant organisms in the almost 25% of the area made up by settlements and croplands (see "artificial" in **Figure 1**). We select the vertebrates that graze 25–34% of the land (Klein Goldewijk et al. 2011) (see "grazer" in **Figure 1**), and we have large impacts through harvesting in the remaining 45% of seminatural and wild land (see "harvest" in **Figure 1**) and, save the area covered by mariculture, in most of the ocean (see "aquatic harvest" in **Figure 1**). Through artificial selection and controlled reproduction of crops, livestock, trees, and microorganisms and by sculpting the new habitats that blanket the planet, humans—directly and indirectly—determine the constitution of species that succeed and fail. This anthropogenic impact on evolution contributes to at least three of five principles defining the Anthropocene biosphere (Williams et al. 2015).

Collectively and individually, then, *Homo sapiens* have set in motion myriad unplanned evolutionary experiments with large impacts at increasingly global scales (Smith et al. 2014). Now is the time to move away from uncoordinated and unmanaged human-driven evolution into conscious stewardship of anthropogenic evolution toward sustainability (**Figure 2**). The areas of governance

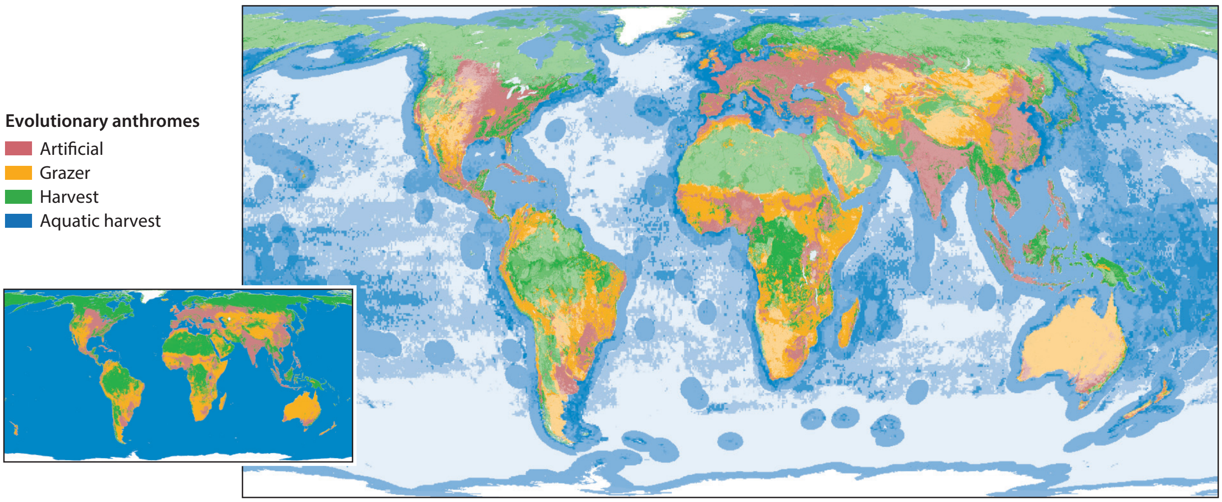

Figure 1

Anthropogenic biomes grouped by type of direct human control of evolution: artificial (*red*), where humans select the main species covering the surface; grazer (*yellow*), where humans control the evolution of the main (often domesticated) herbivorous species; and harvest (*green* on land and *blue* in the ocean), where humans select wildlife through harvesting activities. Darker colors indicate higher intensity of control. Land data reclassified from Ellis et al. (2010) (for further details, see **Supplemental Table 1**). In the ocean, hours of fisheries harvest in 2016 are shown (see also **Figure 3*a***) (Kroodsma et al. 2018) on top of Exclusive Economic Zones (EEZs), in blue. EEZs indicate areas of potential longer-term harvest impacts and some areas not well covered by Kroodsma et al. (2018).

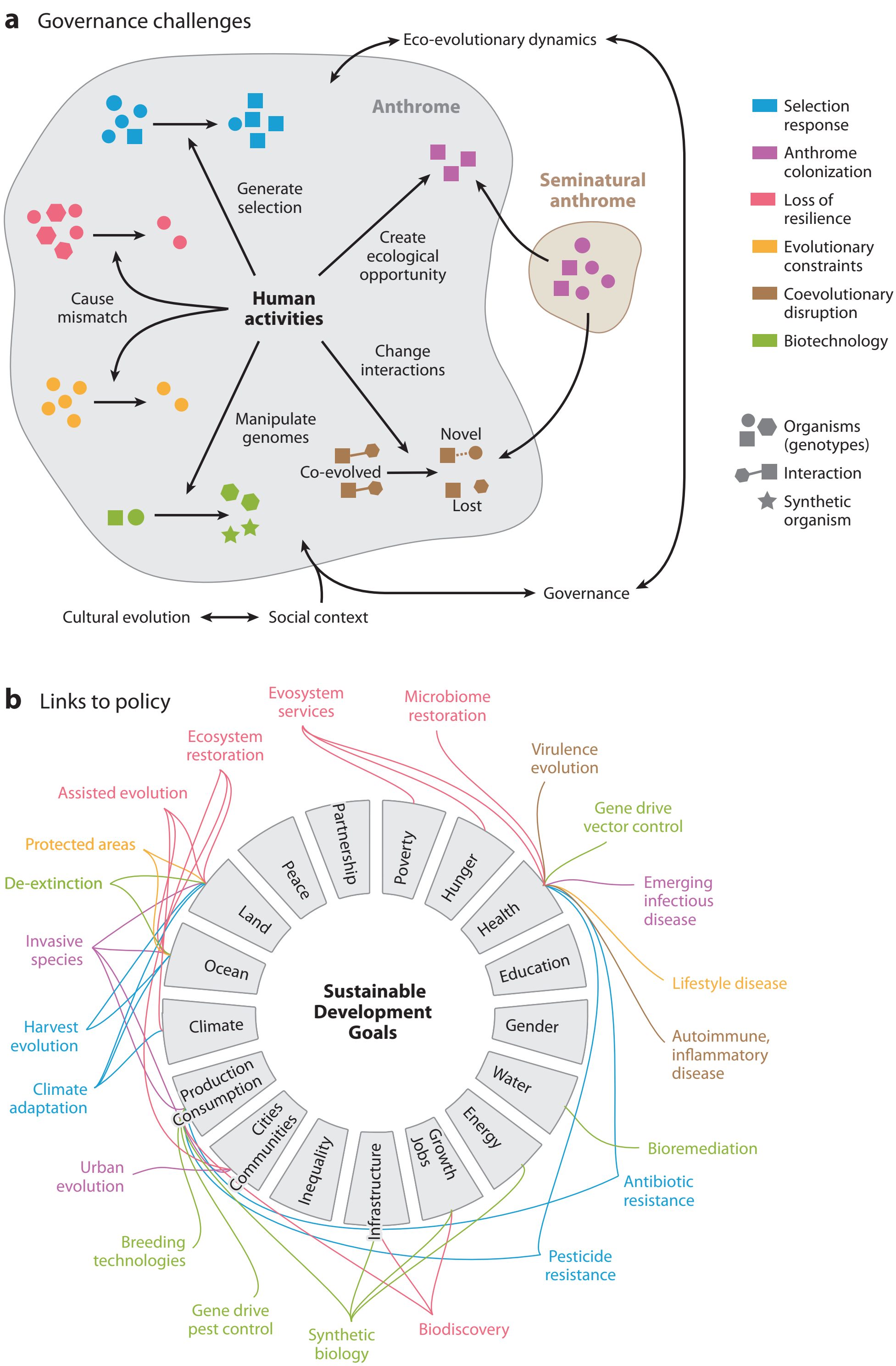

Figure 2

Governance challenges informed by evolutionary biology. (*a*) Dynamics of six governance challenges are sketched with links to human activities. Each example can lead to cross-scale eco-evolutionary dynamics and can be addressed through a variety of governance approaches that must also take their social context into account. (*b*) Color-coded examples of governance challenges and their links to relevant policy domains of the United Nations Sustainable Development Goals (SDGs). Evolutionary perspectives and insights from cultural evolution also inform governance and policies relating to partnerships, peace, inequality, and education but are not a topic of this review. Evosystem services are the contributions of evolution to human well-being.

in which these Anthropogenic evolutionary dynamics are relevant are many. Policy areas influenced by anthropogenic evolutionary dynamics range from agendas for food security, biodiversity conservation, and natural resource management to those for good health for all and safe biotechnology. These areas are major goals or strategies for one of the most central policy objectives of the Anthropocene—namely, achieving sustainable development, as represented by the United Nations Sustainable Development Goals (Carroll et al. 2014) (**Figure 2**). Evolutionary biology is therefore an essential field of research if we are to navigate the Anthropocene successfully.

Policy: a course or principle of action adopted or proposed by an organization or individual

Resilience: the capacity of living systems to sustain key functions in the face of change

Evolutionary constraints: restrictions, limitations, or biases on the course or outcome of adaptive evolution

Mismatch: maladaptive environment for genotypes or phenotypes, referring to a mismatch between historical and current environments

Eco-evolutionary dynamics: the biological dynamics resulting from interaction between ecological and evolutionary processes

In this review, we highlight five overarching Anthropocene challenges for which evolutionary biology is central in informing governance (**Table 1**): (*a*) governing evolutionary feedbacks, (*b*) maintaining resilience and services, (*c*) alleviating evolutionary constraints, (*d*) managing consequences of disrupted coevolution, and (*e*) ensuring safe and successful biotechnology. Despite its importance, in many areas of governance, evolutionary biology has arguably not had an impact that reflects that importance (Carroll et al. 2014). This shortfall is likely due to a mismatch between focus areas of evolutionary biology research and the areas in need of governance and policies (Cook & Sgrò 2017). Due to that disjunction between the centrality of the field and current application needs, we start our review by gauging the development of a policy focus in the contemporary literature of evolutionary biology research and assess priorities and opportunities for increasing the relevance of that research within complex, real-world settings.

2. STATE OF APPLICATION IN GOVERNANCE

Previous reviews of applied evolutionary biology have highlighted a diverse set of applications, including directed evolution and algorithms (Bull & Wichman 2001); solutions for an array of global challenges in food, health, and environment (Carroll et al. 2014); and general applications of evolutionary principles (Hendry et al. 2011). Yet, they have been rather vague about governance and policy implications. The lack of governance and policy focus is also reflected in traditional research journals in evolutionary biology. For example, as per October 10, 2018, out of more than 1,000 published articles in two leading journals (*Evolution* and the *Journal of Evolutionary Biology*), less than a handful (3 and 1, respectively) had "management," "policy," or "governance" in the title. However, signs of attention to governance aspects are emerging, with several journals entirely or partially devoted to applications emerging in the last decade. Since the year 2008, the journal *Evolutionary Applications* has published 82 articles out of 990 meeting our criteria. Importantly, some of these articles are beginning to focus on the needs of decision makers in designing governance strategies and policies enlightened by evolutionary biology (e.g., Cook & Sgrò 2018, Ridley & Alexander 2016).

2.1. Evolution and Governance of Complex Adaptive Systems

Arguably, evolutionary biology has focused on detailing mechanisms for single species in controlled settings, but our general understanding of evolution across communities outside of experimental settings is limited (Barraclough 2015). Several recent reviews have confronted this issue with calls for new types of theories and frameworks to elevate and expand the applications of evolutionary biology, contending with the high levels of uncertainty in complex real-world biological settings with low levels of monitoring (Barraclough 2015, Santamaría & Méndez 2012). These ambitious pursuits are spurring some of the ongoing rapid development of evolutionary biology. In recent decades, the growth of theory around contemporary evolution (Palumbi 2001) and eco-evolutionary dynamics (Hendry 2016) illustrates that considerable evolutionary change can occur over few generations and interact with ecological dynamics.

Table 1 Ways that evolutionary biology informs central governance challenges of the Anthropocene

Dynamics in need of governance	Insight(s)	Governance strategies
Evolutionary feedbacks		
Selection response	Anthropogenic selection is widespread Harvest selection can lead to regime shifts and population collapse	Lower selectivity, monitor trait change, and establish refuges for harvested species
	Resistance to biocides should be expected and resistance management planned for from the start	Promote strategies that combine multiple types of selection (e.g., integrated pest management) Promote specific selection and regulate unspecific selection technologies
Anthrome colonization	Anthromes provide a new ecological opportunity that can facilitate adaptive radiations	Monitor anthrome boundaries with high probabilities of anthrome/biome shift Design settlements and production systems to promote benign species and increase resistance to harmful species
Loss of resilience and services		
Loss of resilience through loss of evolutionary potential	Anthromes are an evolutionary challenge to many species and ecosystems of value	Promote evolutionary potential or functional diversity through phylogenetic or genetic diversity Assist evolution through mixing, moving, or breeding populations
Evolutionary constraints		
Genetic constraints in novel environments	Many species will not be able to evolve through human intervention	Manage environments to resemble those of the evolutionary past Train phenotypes to respond to environment via adaptive immune and cognitive systems
Coevolutionary disruption		
Lost interactions	Many coevolved ecological interactions are being lost, with potential cascading consequences	Protect host species and keystone species by considering effects of policies on microbiomes and other symbionts
Novel interactions	New interactions are more likely to be virulent	Govern the density and connectivity of communities subject to new interactions to lower the probability of both colonization of virulent species and virulence evolution
Safe and successful biotechnology		
Gene drives and genome editing	Genome editing and gene drives potentially have great eco-evolutionary consequences	Regulate use of technologies to promote mutational specificity, evolutionary stability, and termination mechanisms
Synthetic biology and de-extinction	Resurrected species may not be eco-evolutionarily viable	Use extant proxies for extinct species until viability of de-extinct species is likely
Gain-of-function experiments with harmful organisms	Gene flow is a safety risk Evolutionary inquiry is possible through simulations and comparative approaches	Encourage evolutionary inquiry through safe methods rather than evolutionary experiments in harmful species

Evolutionary biology can also make explicit use of frameworks developed to deal with complexity, such as complex adaptive systems (CAS) approaches. In fact, biological systems are classic examples of CAS and display characteristic features of CAS by being path dependent and conditional yet exhibiting repeated higher-level patterns—for example, in the form of convergent evolution of species interactions (Bolnick et al. 2018). Although the type of predictability in CAS is of a different nature to that of deterministic linear systems, it may still be possible to distinguish alternative policies in terms of risk or probabilities of success, even if detailed outcomes cannot be predicted. CAS approaches may help predict diffuse coevolution in complex communities, for example, by focusing on a hub species that affects and connects many species interactions (Toju et al. 2017). The Anthropocene may in fact be viewed as a case of diffuse coevolution, with human society serving as a hub species through which eco-evolutionary dynamics of species-rich communities can be understood.

Complex adaptive systems (CAS): systems in which macroscopic properties emerge from interactions among components and feed back on those lower-level interactions

Convergent evolution: evolution of similar phenotypes or genotypes in multiple independent populations, in response to similar selection pressures, from different initial conditions

Adaptive governance is a general framework for governance of human environment systems confronted with complexity and change (Folke et al. 2005). Adaptive governance deals with fundamental uncertainties through managed experimentation and continuous learning, re-evaluation, and updating of strategies. Generalized evolutionary prescriptions for species conservation have been proposed using an adaptive governance framework (Smith et al. 2014). Design of vaccines for the seasonal flu (Morris et al. 2018) can also be seen as a concrete example of these principles put into practice.

2.2 Factoring in Social Complexity and Cultural Evolution

Governance in the Anthropocene is confronted with equally complex social dynamics (Polasky et al. 2011). In consequence, efforts to inform governance strategies with evolutionary biology must appreciate and take into account the cultural evolution of human behaviors, norms, technologies, and institutions that shape and are shaped by eco-evolutionary dynamics (Creanza et al. 2017) (**Figure 2*a***). Without embracing this social side of the equation, policies will most likely be unsuccessful due to design failure. An example of how some evolutionarily informed governance strategies work in theory, but less well in practice, is agricultural pesticide use, in which a contributor to rapid evolution of pesticide resistance is the social transmission of farmer overreliance on pesticides (Dentzman et al. 2016). Hence, when resistance evolves, the response of farmers—complying with prevalent norms—matters for the future trajectory of evolution. Similarly, policies for pesticide resistance management that do not take regional differences in regulatory enforcement into account are less likely to live up to predictions of evolutionary optimal strategies (Living with Resistance project 2018). When understood well, such social dynamics can be a policy lever for governing evolutionary challenges, such as antibiotic resistance (Hallsworth et al. 2016).

3. GOVERNING EVOLUTIONARY FEEDBACKS

Evolutionary feedback to human activities is perhaps the most urgent governance challenge informed by evolutionary biology across policy domains (cf. "selection response" and "anthrome colonization" in **Figure 2*b***). Here, we focus on two types of feedback: (*a*) responses to human-driven selection within Anthropocene habitats and (*b*) colonization of Anthropocene habitats (**Figure 3**). These two feedbacks often interact, but here we treat them separately for clarity (Reznick & Ghalambor 2001).

3.1. Responses to Widespread Selection

Human activities are major sources of selection and contemporary evolution for species that live in affected habitats, but these effects often go unnoticed (Alberti et al. 2017, Reznick &

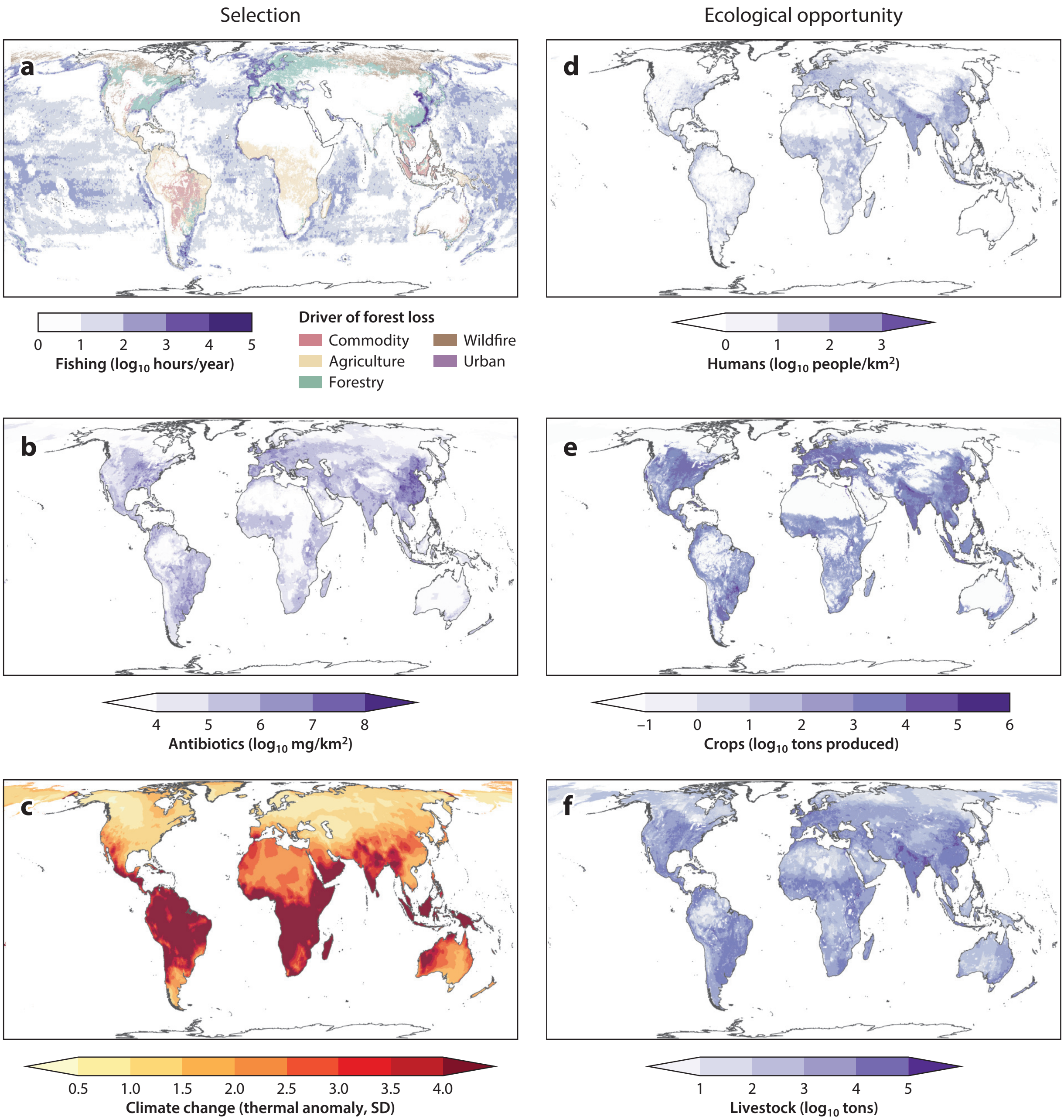

Figure 3

Anthropocene selection and ecological opportunity in the twenty-first century. Panels display selection from (*a*) fisheries harvesting (hours per year; Kroodsma et al. 2018) and drivers of deforestation (Curtis et al. 2018), (*b*) livestock-associated antibiotic use (Van Boeckel et al. 2015), and (*c*) climate change [standardized temperature anomalies in standard deviations (SD) (Garcia et al. 2014)] and ecological opportunity presented by (*d*) human population (CIESIN 2017), (*e*) harvested crop biomass (Monfreda et al. 2008), and (*f*) livestock biomass (Robinson et al. 2014). All data sets, except climate change and forest loss, are presented at a logarithmic scale with base 10.

Ghalambor 2001) (**Figure 3*a–c***). In particular need of governance are situations in which (*a*) valued species and communities of concern are unable to respond to selection (see Sections 4 and 5) or (*b*) respond in undesirable ways, and situations in which (*c*) species of potential harm respond in ways that increase their threat (Carroll et al. 2014). Evolutionary adaptation to human selection and to Anthropocene habitats by gains in defense functions—resistance evolution—are two major examples of the second and third situations, respectively.

Biocide: a chemical substance intended to exert a controlling effect on any harmful organism; includes antimicrobials and pesticides

3.1.1. Harvest evolution as early warning of change. Many species have evolved to evade human harvest, whether through behavioral evolution, evolution of smaller size to avoid traps, or evolution of features that make them less attractive to hunters (Darimont et al. 2009, Sih et al. 2011). The impact of this type of harvest evolution on society is—when documented—relatively small. For example, the economic impact of evolution toward smaller body size in harvested fish species has been argued to be of minor economic impact compared with the decline in population size induced by harvesting (Heino et al. 2015). Similarly, harvest-induced evolution in wild species has rarely been documented to have a negative impact on species that we want to protect but may instead actually improve their chances of survival—as in cases of smaller antler size or loss of tusks, which reduce desirability for trophy hunters (Chiyo et al. 2015). However, larger scale consequences of harvest-induced trait changes cannot be ruled out and may alter trophic cascades, nutrient cycling, and ecosystem stability, especially when harvesting targets ecosystem engineers or keystone species (Palkovacs et al. 2018). In such cases, evolution in harvested populations should be monitored closely and may act as early warning signals of population collapse or ecosystem regime shifts (Palkovacs et al. 2018). Strategies for minimizing these negative consequences include decreasing harvest rates and their selectivity and establishing refuges from which gene flow of nonharvested populations can mitigate change (Palkovacs et al. 2018).

3.1.2. De-escalating biocide resistance. Resistance evolution poses increasing risks to production ecosystems, human health, and environmental management, in particular through biocide resistance evolution to pesticides and antimicrobial compounds (Carroll et al. 2014). The scale of this governance challenge is significant. Antibiotic resistance is among the world's most significant health threats, cancer resistance is a contributing factor to relapse, antiviral and antimalarial resistance threatens treatments of major diseases, and pesticide resistance is a growing concern for agricultural systems, humans, and wildlife (Lipinski et al. 2016, Living with Resistance project 2018, Rev. Antimicrob. Resist. 2016). Evolution of resistance is itself associated with ecological properties, such as species richness and community composition, that help regulate ecosystem services, such as pollination, biological control, and immune and digestive function (Living with Resistance project 2018).

Resistance to biocidal technologies should always be anticipated, especially when targeted populations are large and diverse or connectivity is high to other treated environments (Living with Resistance project 2018). Preventing resistance by varying and diversifying chemical selection has been the object of studies for decades, but except in cases of strictly enforced regulation and simple ecosystems, this strategy can only delay resistance (Living with Resistance project 2018). In contrast, multimodal control strategies impose less directional selection for resistance and diversify the set of traits that are exposed to selection, thereby lowering rates of adaptation (Carroll et al. 2014). In agriculture, integrated pest management has become the modern exemplification of such strategies, making use of a range of tactics, including mechanical and chemical control, and increasing spatiotemporal variation in habitats and control mechanisms (Carríere et al. 2019) (**Figure 4*a***).

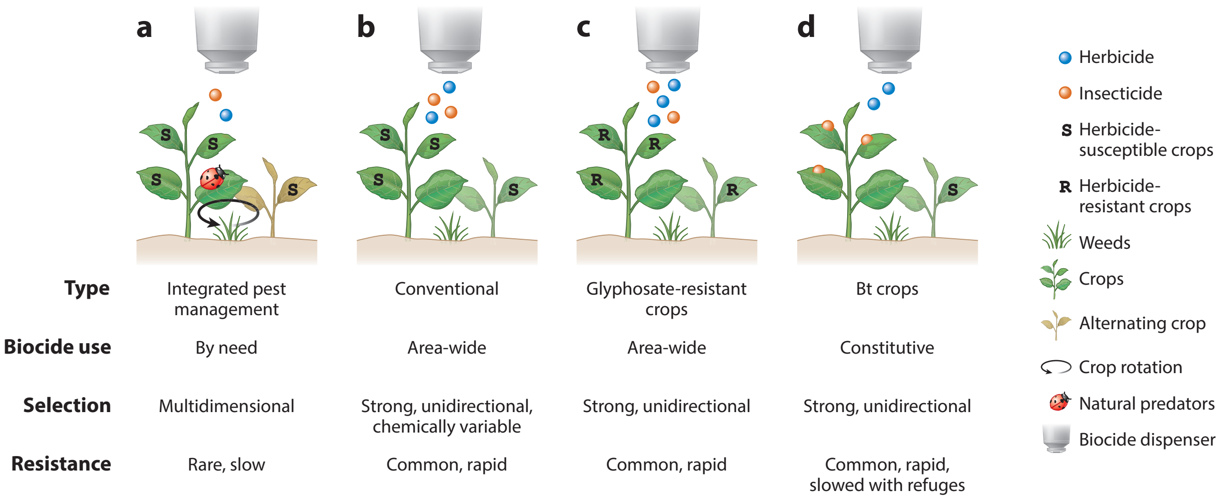

Figure 4

Archetypical characterizations of selection dynamics in four major crop pest management strategies. (*a*) Diverse integrated pest management tactics impede pest adaptation. (*b*) Conventional toxic chemical sprays select efficiently for multiple resistance. (*c*) Narrow reliance on glyphosate application in glyphosate-resistant crops has generated a surge in resistance and escalated glyphosate dosing. (*d*) Endogenous insecticidal *Bacillus thuringiensis* (Bt) toxins create invariant selection, but mandated refuge plantings of susceptible crops have slowed resistance by breeding wild types to mate with and genetically neutralize the rare resistant individuals that mature on nearby Bt plants.

A key governance priority is the promotion of strategies that do not lead to escalation-prone arms races between mounting levels and modes of resistance and increasing dosing or shifts to less desirable biocides (Living with Resistance project 2018). The adoption of transgenic (tg) crops with insecticidal *Bacillus thuringiensis* (Bt) toxins or glyphosate-resistant (GR) genes illustrates how paying closer attention to simple principles of how selection is applied could help avoid unnecessary escalation in the future (**Figure 4*c*–*d***). GR crops allow farmers to apply glyphosate more indiscriminately (**Figure 4*c***). However, insecticidal Bt crops—crops with an insecticidal gene inserted—help increase the specificity of selection by exposing only insects feeding on specific parts of the crops (Carríere et al. 2019) (**Figure 4*d***). Although both types of tg crops have seen resistance evolve, resistant weeds in fields of GR crops have spread particularly rapidly (Heap & Duke 2018). Insects have also evolved resistance to Bt crops in several regions but overall to a lesser extent, and when strictly enforced, non-Bt refuges provide a strategy to significantly slow or even avoid resistance evolution (Carríere et al. 2019). Similar governance alternatives exist for cancer treatment such as adaptive therapy and immunotherapy, which help lower selection from traditional chemotherapy and radiation therapy (Gatenby et al. 2009, Sharma et al. 2017).

3.2. Colonization of Anthromes

Although hostile to a majority of species, the large area covered by anthromes with a substantial degree of human transformation (**Figure 1**) also presents a vast ecological opportunity for colonizing species (**Figure 3*d*–*f***). This opportunity is what evolutionary biology predicts to be the foundation for adaptive radiations (Stroud & Losos 2016). In fact, the prelude to the adaptive radiation that also succeeded all previous mass extinctions has already begun at a small scale in response to the current Anthropocene extinction crisis (Thomas 2015), although it will presumably take millions of years for this radiation to rebuild past levels of diversity (Davis et al. 2018). Colonizing species can have substantial impact on society and are therefore of high governance priority. Emerging infectious diseases (EIDs) and invasive species, for example, have a major impact on human health, livestock, and wildlife (Allen et al. 2017).

Phylogenetic diversity (PD): a measure of biodiversity that incorporates phylogenetic difference between species (e.g., measured as the sum of branch lengths)

Evolutionary biology offers an analytical toolkit for predicting the types of species that will succeed evolutionarily in Anthropocene habitats and where new species are likely to appear. One framework for predicting biome shifts in plants identifies the major traits of species and habitats most likely to be sources and destinations of colonization (Donoghue & Edwards 2014). Colonizing species are likely to have (*a*) large population size, (*b*) short generation time and high mutation rates, (*c*) preadaptation and access to these enabler adaptations, (*d*) been exposed to changing environments, and (*e*) exhibited previous biome shifts (Donoghue & Edwards 2014). Biome shifts can be expected (*a*) into larger biomes with ecological opportunity, such as few competitors or natural enemies; (*b*) out of large and biodiverse biomes; (*c*) between biomes that have been in direct contact for considerable time; or (*d*) between a retreating edge of an old biome and an expanding edge of a new, opportune biome (Donoghue & Edwards 2014). Importantly, in the Anthropocene, adjacency of biomes does not need to be through geographical proximity but can also be through trade and travel linkages (Living with Resistance project 2018). Incomplete lineage sorting, adaptive introgression, and hybridization are likely to be important processes, as they have been in other recent radiations (Henning & Meyer 2014, Thomas 2015).

Recent analyses of EIDs support several factors in the colonization framework given above. Zoonotic disease hot spots are likely to be tropical forest regions with high levels of mammal diversity and experiencing land use change (Allen et al. 2017, Jones et al. 2008). General evidence has also been found that zoonoses emerge at the nexus between natural habitats, human settlements, agriculture, and livestock (Jones et al. 2013, Parnell et al. 2017). Further, RNA viruses with high mutation rates are overrepresented among EIDs, indirectly supporting genetic access to a diversity of adaptations and large population size as predictors (Firth & Lipkin 2013). These results give reason for general optimism about the ability of refined frameworks to inform governance of anthrome colonization.

4. GOVERNING RESILIENCE AND SERVICES

We have so far dealt with the governance of rapid eco-evolutionary change, but evolutionary biology provides equally powerful insights and tools for managing resilience and ecosystem services of species and ecosystems that struggle to adapt in the Anthropocene (Carroll et al. 2014, Folke et al. 2004) (**Figure 2*a***), including those under human control and human beings ourselves. Many strands of evolutionary biology predict that the species and ecosystems most vulnerable in the Anthropocene are those that have evolved in comparatively stable environments, have low population size, have little genetic variation, are spatially fragmented, are at the limit of fundamental genetic constraints, and are exposed to rapidly changing and fundamentally novel environments (Carroll et al. 2014, Hoffmann & Sgrò 2011, Lankau et al. 2011).

4.1. Genetic Variation as a Priority for Resilience

As many species will need to adapt evolutionarily to thrive in the Anthropocene (Bell 2017), a key principle for managing resilience has been to preserve genetic diversity (Sgrò et al. 2011, Smith et al. 2014). Similarly, at the ecosystem level, phylogenetic diversity (PD) of ecological assemblages has been proposed as a key metric for the resilience of ecosystem function (Faith et al. 2010) and as an indicator for assessing ecosystem vulnerability to environmental change (Díaz et al. 2013). However, the uncertainty around the correlation between PD, functional diversity, and evolutionary potential poses challenges (Winter et al. 2013). So does developing the capacities to distinguish between general genetic variation and variation that will be critical for adaptation in the increasing wealth of genetic data (Pearse 2016). To preserve resilience at the macroevolutionary level, protected area allocation could aim to prioritize PD (Faith et al. 2010). At the intraspecific level, areas with high genetic diversity could be prioritized and, indeed, may sometimes be able to predict ranges of other threatened species (Smith et al. 2014). The use of phylogenetic analysis can also be extended to other policy and governance areas. Phylogenetic tools can help predict where discovery of new chemical compounds in the tree of life will be successful. For example, in the South African fynbos, PD predicts ecosystem services such as medically useful plants and economic value (Forest et al. 2007). In human production systems, considering PD or functional diversity is important in the selection of organisms for seeds banks, botanic gardens, and preservation in the wild (Castañeda-Álvarez et al. 2016).

Evolutionary potential: ability to adapt evolutionarily to one or multiple environments

4.2. Building Resilience Through Translocation and Assisted Evolution

Resilience can be manipulated through two basic types of intervention common in species under human control, namely moving and mixing populations in places that better match their evolved niches or through actively assisted evolution involving breeding or genetic engineering (Carroll et al. 2014). There are increasing calls for a more active role of conservation policy in enhancing resilience of wild species through these strategies (Frankham et al. 2017, Sgrò et al. 2011, Smith et al. 2014, van Oppen et al. 2015). For example, coral reef resilience may have to be strengthened through human-assisted evolution, given projections of insufficient in situ responses (van Oppen et al. 2015). Examples of assisted evolution include inducing phenotypic acclimatization through exposure to anthropogenic environmental conditions, introduction of stress-tolerant symbionts, and selectively bred or experimentally evolved species (van Oppen et al. 2015). Similarly, assisted migration and evolution of trees have been suggested to help build evolutionary resilience to climate change (Aitken & Bemmels 2016), diseases, and pests (Sniezko & Koch 2017) and will likely be central in efforts to meet the 1.5°C target (IPCC 2018). Ecosystem restoration increasingly needs to consider evolutionary dynamics to ensure long-term resilience of restored communities (Lau et al. 2019, Raimundo et al. 2018, Sgrò et al. 2011).

5. GOVERNING EVOLUTIONARY CONSTRAINTS

Sometimes the resilience of species and ecosystems cannot be enhanced by increasing their evolutionary potential, for reasons that include fundamental biological, as well as ethical and legal, constraints and concerns (**Figure 2*a***). For example, fundamental boundaries of climate evolution appear to exist or be shared among distantly related species (Araújo et al. 2013), and the widespread exposure to novel environments can create both ecological and evolutionary traps (Robertson et al. 2013). A set of governance interventions is available to alleviate evolutionary constraints. Organisms or ecosystems can be moved to suitable environments (see Section 4), the environment can be changed on-site to better fit evolved niches, or the phenotypic response to the environment can be altered by training evolved phenotypic reaction norms—for example, through vaccination, physiological acclimatization, or learning (Carroll et al. 2014). In the context of new Anthropocene environments, we focus on altering the environment to better fit evolved niches, which is fundamental to conservation biology, public health, and medicine, as it underlies environmental management of threatened species and ecosystems (Ashley et al. 2003) as well as interventions to improve human health in the face of environmental pollution and lifestyle disease (Wells et al. 2017). For example, many human diseases are thought to originate from mismatches to the new Anthropocene environments, such as type 2 diabetes with high availability of glucose (Goh et al. 2014).

Nonparallel evolution: spectrum spanning from convergent to divergent evolution, the latter consisting of evolution of increased phenotypic or genotypic distance between populations

Hygiene and biodiversity hypotheses: two related hypotheses that reduced contact of people with the natural environment adversely affects the immunomodulatory capacity of human microbiota

Hologenome: the collective genomes of a host organism and its symbionts

Adaptive networks: networks in which the feedback between the dynamics of species interaction structure and population-level processes shapes interactions, abundances, and traits

Three types of analysis can help predict species in need of management due to lack of adaptation and phenotype–environment mismatch: (*a*) analysis of evolutionary history (Ashley et al. 2003, Gluckman et al. 2011), (*b*) analysis of environmental exposures early in life (Gluckman et al. 2011), and (*c*) association analysis of genomic, phenotypic, and environmental exposure databases (Denny et al. 2013). Although the former two approaches are long established in evolutionary biology, the last has gained recent interest for disentangling environmental and evolutionary phenotypic contributions using, for example, public health register databases (Denny et al. 2013). These analyses can speed diagnosis, and even if a course of disease is not altered, attention can shift to treating the individual rather than continuing the diagnostics process and can help drive down rapidly increasing costs of developing therapeutics (Denny et al. 2016). However, some caution about the evolutionary insights that these association studies can provide is needed. In ecological settings, the complex regulation of many phenotypes, including through epistatic interactions between many genes and phenotypic plasticity, challenges the applicability of association studies (Shaw 2019). In human health settings, the many genetic conditions without a specific intervention limits options for acting on association studies (Strande & Berg 2016). Due to the prevalence of convergent and nonparallel evolution (Bolnick et al. 2018), it is important not to extrapolate beyond geographical populations. In humans, advancing knowledge of less-studied non-Western genotypes is needed (Adhikari et al. 2017). For example, lactose tolerance is monogenic in Europe but often polygenic and less well understood in other regions (Ségurel & Bon 2017).

In a cautionary example epitomizing the practical challenges of governing evolutionary constraints, the endangered Iberian lynx (*Felis pardinus*) cannot escape its remnant habitat to recolonize its former range. Assisted reintroduction is hampered by the decimation of its native rabbit prey by introduced biocontrol viruses (Ferreira & Delibes-Mateos 2011). A desperate annual vaccination program to adapt rabbit pups is difficult to complete before the annual summer virus outbreak, after which vaccinating exposed pups increases their mortality, leaving the efficacy of this intervention in question (Rouco et al. 2016).

6. GOVERNING COEVOLUTIONARY DISRUPTION

Ongoing coevolutionary processes underlie the stability of ecological communities (Lankau 2011) and hence the resilience of ecosystems and the Earth's biosphere. Yet, human transformation of the planet is disrupting and altering existing interactions and creating new ones that lack coevolutionary history (**Figure 2*a***). Disruption occurs through local extinction of a variety of interactions (Valiente-Banuet et al. 2015) and the emergence of new interactions—for example, via colonization of anthromes (see Section 2). These developments have significant impact on topics of societal concern, including human health (Allen et al. 2017, von Hertzen et al. 2015), biodiversity conservation (Colwell et al. 2012, Vredenburg et al. 2010), and food and biomass production (Jones et al. 2013, Motta et al. 2018). Evolutionary biology informs these challenges through hypotheses, such as the hygiene and biodiversity hypotheses (Brooks et al. 2013, von Hertzen et al. 2015); concepts, such as the hologenome concept (Bordenstein & Theis 2015); and theory, such as the adaptive networks theory (Raimundo et al. 2018). A particular worry is that disruption of coevolved symbioses can lead to cascading ecosystem perturbations. Integration of microbiome data means that we increasingly think about most organisms, including humans, as multispecies symbioses, with the microbiome viewed as a second genome (Foster et al. 2017). Exposure of honeybee microbiomes to glyphosate is possibly contributing to honeybee colony collapse disorder (Motta et al. 2018), and disrupted human microbiomes likely play a role in autoimmune and inflammatory diseases (von Hertzen et al. 2015).

Novel interactions, which have not been subject to coevolution, are more likely to be hostile (i.e., virulent) to one or more species (Ewald 1994, 2011; Lebarbenchon et al. 2008). This is particularly the case in high-density, high-connectivity ecosystems as new species are under little selective pressure to adapt to the new easy-to-colonize habitat in ways that reduce their impact (Ewald 1994, Jones et al. 2013). This insight has broad implications for design and governance of many human production ecosystems (Jones et al. 2013) and human settlements (Ewald 2011) where these properties relax negative selection on virulence (Jones et al. 2013).

Gene editing: targeted manipulation of a specific site of the genome of a living organism by deletion, replacement, or insertion

7. GOVERNING BIOTECHNOLOGY

A defining principle of the Anthropocene is that the technology of one species, humans, is actively modifying a major portion of other living organisms on the planet (Gillings & Westoby 2014, Williams et al. 2015). Evolutionary biology informs the governance of biotechnology, including the identification of risks, benefits, and priority applications (Bevan et al. 2017). This process includes guiding the development of biotechnology to circumvent existing evolutionary trade-offs (Denison 2011). However, informing governance of current technologies has become increasingly difficult given rapidly advancing capabilities in construction and engineering (synthetic biology), precise editing (genome editing), and potential rapid spread (gene drives) (Drinkwater et al. 2014, Wright et al. 2013). These challenges include the lack of comparison with wild types, risk of genetic instability, and lateral gene transfer in the environment (Drinkwater et al. 2014).

7.1. Gene Editing and Gene Drives

Two new features illustrating the increasing scope for human biotechnology are the use of gene drives that can spread a mutation through an entire population of sexually reproducing organisms (Noble et al. 2017) and gene editing (with CRISPR/Cas9) that increases the array of traits that can be altered, inserted, or deleted with comparatively high precision (Singh et al. 2017). When combined, gene drives and gene editing technology have the potential to spread specific genes in populations at an unprecedented pace and level of control; therefore, concerns have been raised about their safe use and governance (Akbari et al. 2015, Jasanoff & Hurlbut 2018). Particular worries are that these systems may mutate, be transmitted to nontarget organisms, be used in a damaging way by promoting dangerous or impeding valuable species, or have hard-to-predict eco-evolutionary consequences in the wild (Drinkwater et al. 2014). Gene drives in mosquitos (Kyrou et al. 2018) and mice (Grunwald et al. 2019) have recently been tested in laboratory settings but are not immune to evolution of resistance in the wild (Unckless et al. 2017). Tests in larger confined areas will show if changes in relative fitness under competition for resources are large enough to select for resistance (Kyrou et al. 2018). A major priority before testing in the wild is the construction of evolutionarily stable mechanisms for such tg organisms to become inviable, so-called kill switches (Wright et al. 2013). With these gaps in the technology still missing, the world's governments have recently agreed to limit the use of gene drives in the wild (Callaway 2018). In humans and threatened wildlife, one of the main evolutionary challenges—besides many ethical concerns—is increasing the specificity of gene editing (Xiong et al. 2016).

7.2. Synthetic Biology and De-Extinction

Synthetic biology is the exercise of engineering new or partially new living systems. It is currently being discussed as a technology that could help halt and even reverse the loss of biodiversity, including through de-extinction, but little engagement exists between the conservation and the synthetic biology communities (Piaggio et al. 2017). From an evolutionary perspective, significant concerns are that resurrected species are likely to have low evolutionary resilience (e.g., low genetic diversity) and be poorly adapted to both the biotic and abiotic changes that occurred since their extinction and the environment into which they are introduced (Robert et al. 2017). For example, the absence of coevolved mutualistic and parasitic microorganisms could be a problem for the viability of de-extinct species, as with time they would be exposed to colonization of new, perhaps virulent, species (Selbach et al. 2018). The practical challenges of bringing evolutionarily viable species back from extinction may be so large (even for recent extinctions) and potentially harmful for efforts to preserve threatened extant species (Bennett et al. 2017) that using functional proxies for extinct species may be a more viable, yet still challenging, approach (Steeves et al. 2017). The challenge of bringing back extinct species or replacing their functions only adds weight to the ethical argument for preventing species extinctions.

Gain-of-function (GOF) experiments: broadly defined as experiments expected to increase the transmissibility or virulence of pathogens

Transdisciplinary research: knowledge coproduction between researchers and other individuals or organizations in society

7.3. Safer Alternatives to Risky Experiments

A debate about the safety of so-called gain-of-function (GOF) experiments with potential pandemic pathogens (PPPs) emerged after the publication of two articles describing the creation of highly pathogenic viruses with airborne transmission and following reconstruction of the 1918 H1N1 pandemic influenza virus (Lipsitch 2018). Given the tremendous global risks with such experiments, it is desirable to use safer alternatives to inform governance, including evolutionary modeling and comparative approaches (Lipsitch 2018). Beyond the GOF PPP debate and stemming from the above discussion, evolutionarily safer applications of biotechnology are those that do not exert broad selection; do not disrupt or create new ecological interactions; are used at a limited extent; and have multiple mechanisms for termination.

8. ANTHROPOCENE (CO)EVOLUTION AND TRANSDISCIPLINARITY

As we have seen, evolutionary biology informs governance of both contemporary evolution and lack thereof, from the level of the gene to the level of the planet, across sectors of society. In our review, we have emphasized five common challenges of biosphere governance in the Anthropocene that evolutionary biology informs, namely (*a*) governing evolutionary feedbacks, (*b*) maintaining resilience and services, (*c*) alleviating evolutionary constraints, (*d*) managing consequences of disrupted coevolution, and (*e*) ensuring safe and successful biotechnology. In reality, these five challenges occur in parallel and interact, and decision-making will have to consider this added complexity in almost every situation. Doing so will be made easier by addressing three priorities.

First, developing a coherent theory of evolution in the Anthropocene that considers the eco-evolutionary dynamics humans are impacted by, are part of, and drive. This step entails better integration of the features defining the Anthropocene biosphere (Williams et al. 2015) and the adaptation of existing evolutionary theory to more explicitly consider the role of humans in evolution, instead of treating anthropogenic change and control as passive processes (Gillings & Westoby 2014).

Second, appreciating that governance of eco-evolutionary dynamics in the Anthropocene occurs in contexts of diverse social dynamics that can be used as leverage points for intervention (Brooks et al. 2018). This priority points toward the need for a field of coevolutionary governance of intertwined cultural and organic evolution to inform decision-making, management, and policy.

Third and finally, nurturing a culture of transdisciplinary research in evolutionary biology will help bridge the current policy gap by informing evolutionists about the complex governance context of decision makers and the critical information they need to inform decisions. Signs of such engagements are already emerging, whether in hospital therapy (Woods & Read 2015) or in design of conservation strategies and policies (Cook & Sgrò 2018, Ridley & Alexander 2016). Naturally, this engagement will also help build trust and make decision makers more interested in the power of evolutionary inquiry for biosphere stewardship in the Anthropocene era.

SUMMARY POINTS

1. Evolutionary biology is an essential field for the successful governance of living systems in the Anthropocene. However, evolutionarily informed decision-making is limited by the lack of information and the lack of theory to inform governance of complex adaptive systems with high levels of uncertainty and complex social dynamics.
2. Evolutionary biology helps select de-escalatory strategies that avoid undesirable evolution and arms races in response to widespread anthropogenic selection and—when widespread selection cannot be avoided—helps vary and apply selection in ways that hinder unwanted responses, such as biocide resistance.
3. Evolutionary biology predicts where adaptive colonization of human transformed habitats is most likely. These insights are critical components informing design of monitoring strategies for emerging infectious diseases and managing general anthrome colonization.
4. Preservation of resilience and ecosystem services of many species and ecosystems can be achieved by incorporating indicators of evolutionary potential into governance or by creating interventions that enhance potential for, or directly assist, adaptive evolution.
5. When evolutionary adaptation is not possible or desirable, evolutionary constraints can be governed by managing the environment to better fit historical environments where species evolved or by training adaptive subsystems such as immune systems, physiological systems, or cognitive systems.
6. Disruption of coevolved interactions can have cascading consequences for ecosystem function and human health, and protecting host–microbiome interactions is an urgent priority in all areas of governance, for example, by considering adaptive networks. Novel interactions, likely to be more virulent, should be monitored for in high-risk zones, and system features, such as density and connectivity, should be governed in urban areas and production ecosystems to lower probabilities of new virulent interactions.
7. Evolutionarily informed governance of biotechnology's rapidly expanding abilities to construct and manipulate living systems is urgently needed, including in the context of genome editing, gene drives, synthetic biology, and experiments with potential serious and widespread consequences. Mutational specificity, evolutionary stability, termination mechanisms, evolutionary safe alternatives, and eco-evolutionary viability are key principles to inform policies.

DISCLOSURE STATEMENT

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