Coevolutionary Governance of Antibiotic and Pesticide Resistance

Development of new biocides has dominated human responses to evolution of antibiotic and pesticide resistance. Increasing and uniform biocide use, the spread of resistance genes, and the lack of new classes of compounds indicate the importance of navigating toward more sustainable coevolutionary dynamics between human culture and species that evolve resistance. To inform this challenge, we introduce the concept of coevolutionary governance and propose three priorities for its implementation: (i) new norms and mental models for lowering use, (ii) diversifying practices to reduce directional selection, and (iii) investment in collective action institutions to govern connectivity. We highlight the availability of solutions that facilitate broader sustainable development, which for antibiotic resistance include improved sanitation and hygiene, strong health systems, and decreased meat consumption.

Coevolution in the Anthropocene

Humans’ role as the strongest evolutionary force on Earth [1] results in widespread ecoevolutionary environmental change [2], a defining feature of the Anthropocene biosphere [3] with large implications for policy and governance [4,5]. Genetic evolution is now shaped by human actions, ranging from the level of the gene to that of the biosphere [1,4–6]. At the same time, human cultural evolution operates in a new context of a globally interconnected world with unprecedented capacity for communication and speed of change [7–9]. Cultural change not only is a driver of, but is itself shaped by ongoing environmental change [10,11].

The combination of human cultural and environmental ecoevolutionary dynamics manifests in human–environment coevolution between human social systems and the environment [10,11] (Figure 1). The term ‘coevolution’ was originally applied to studies of interdependent Darwinian evolution of pairs, groups, or communities of species [4,12,13], but with the advent of theory for cultural evolution, the use of the term has been expanded to studies of how culture and genes coevolve within a species [8,14,15] (Figure 1). More recent advances in the study of ecoevolutionary dynamics [2] and theories of nongenetic evolutionary change [15] emphasise the utility of recasting human–environment coevolution in terms of two sets of interacting multilevel ecoevolutionary dynamics (Figure 1, Text S1 in the supplemental information online).

The trajectory of human–environment coevolution is not predetermined but is path-dependent and can proceed along several trajectories, depending on how and whether it is governed by humans. However, coevolution is poorly integrated into current governance theories for studying how societies, at all levels, steer themselves toward desirable ends. To provide a venue for such integration, we introduce the concept of ‘coevolutionary governance,’ which is...
the explicit governance of human–environment coevolution [4]. Coevolutionary governance is related to but distinct from adaptive [16] and other forms of anticipatory governance [17] in that it recognises to a larger extent, anticipates, and explicitly analyses these interdependent ecodevelopmental dynamics in its attempt to guide human societies toward identified goals [4].

We highlight the value and insights of coevolutionary governance through two classical examples of human–environment coevolution: that of human antibiotic and pesticide use and the evolution of resistance to these compounds. In this paper, we refer to these compounds collectively as ‘biocides.’ Modern health systems and production of food, fuel, and fibre are reliant on biocides for controlling unwanted microorganisms, arthropods, and plants with which human societies have coevolved [5,10]. However, biocide resistance is an increasing risk, with multiple resistance to antibiotics, insecticides, and herbicides on the rise [5,18]. Antibiotic resistance is associated with hundreds of thousands of deaths per year [19], and insecticide and herbicide resistance is a potential threat to food, fuel, and fibre security that also entails economic losses for farmers and health risks from exposure to increasing pesticide use [5,20,21]. Not only are levels of resistance to a much wider array of compounds now much higher, but for both antibiotics and pesticides, there are declining prospects for developing more conventional compounds in the next decades [22]. Simultaneously, the next decade will be critical for meeting a set of interconnected global environmental and societal challenges captured in part by the 17 Sustainable Development Goals (SDGs; https://sustainabledevelopment.un.org/sdgs) put forth by the United Nations [5].

Rising resistance levels are evolutionary consequences of widespread practices employed to control pests and pathogens [1,5,8,22] (Figure 1), and resistance is therefore unlikely to be solved through quick fixes. Rather, it represents the dual challenge of governing coevolution between human culture and species targeted for control with strategies that cofacilitate broader goals of sustainable development [5,8,10,23]. After reviewing the emerging global dynamics of biocide use and resistance, we identify priorities for coevolutionary governance of biocide resistance and then focus on the challenges of promoting them in the context of the SDGs. We believe that coevolutionary governance has the potential to help promote successful transformations to sustainability in the Anthropocene biosphere by, for example, stimulating the evolution of norms and technology for sustainability.

The Global Dynamics of Resistance

The global dynamics of resistance evolution can be characterised by the scale, intensity, and composition of biocide use, as well as the spatial extent of biocide gene exchange. Over the past 30 years, antibiotics, insecticides, and herbicides have undergone major changes in these four aspects and present both unique and shared governance challenges (Figure 2). For all three biocides, scale of use – indicating global selection for resistance – has increased markedly since monitoring began (Figure 2A,D,G). Only conventional insecticide use has started to decline as transgenic crops producing the insecticidal *Bacillus thuringiensis* proteins (Bt crops) replace conventional insecticides and as integrated pest management (IPM) is implemented [20,24].

Global trends in biocide use intensity imply changes in local selection for resistance and are highly divergent between the three types of biocides. Human antibiotic use (monitored mainly via pharmaceutical sales) has increased by 36% since 2000 [25] (Figure 2B). Although similar global scale monitoring is lacking in important high-use environments such as communities and hospitals as well as animal farming, available regional data show that antibiotic use for animals...
Figure 1. Governing Coevolution. (A) Conceptual illustration of some of the major types of coevolution and the direct and indirect effects of coevolutionary governance of human–environment coevolution. Eco-evolutionary dynamics take place both within and between the cultural and environmental sub-systems with some of their major levels indicated in the figure. (B) Priorities for coevolutionary governance of biocide resistance include (i) reducing use by shifting mental models and social norms for what might be likely and desirable solutions (blue); (ii) systematically diversifying practices, including by integrating selected past practices with new technologies (green); and (iii) governing local to global connectivity through collective action institutions (yellow). Implementation of these priorities will help decrease biocide use and manage resistance in a highly connected world (see Spatial dynamics).
varies widely among countries [26]. Conventional insecticide sales per agricultural area have dropped more than 10% over the past 5 years and are now below levels from the 1990s (Figure 2H). In contrast, herbicide sales per area have increased by 70% (Figure 2E). These...
diverging trends are in part explained by adoption of transgenic crops: Insecticidal Bt crops helped reduce use of conventional insecticides [20], whereas glyphosate-resistant crops encouraged a 15-fold increase in the use of glyphosate, driving the herbicide trend [27] (Figure 2D,F,I).

Biocide use can become uniform through widespread adoption of successful compounds, but the large area across which selection occurs also makes such biocides vulnerable to resistance. The adoption of transgenic crops has homogenised selection pressures through increasing uniformity of pesticide use and of pest management in general. Today transgenic crops make up more than 30% (glyphosate-resistant crops) and 15% (Bt crops) of the planted area of certain crops, such as corn, cotton, and soybean, worldwide (Figure 2F,I) and more than 90% in some of the largest-producing countries [28]. Similarly, as low- and middle-income countries (LMICs) have seen economic growth, their use of antibiotics has increased dramatically, leading to a global convergence in antibiotic use [25].

Resistance can spread rapidly in highly connected systems. Historical efforts to govern antibiotic resistance have, for good reasons, largely focused on managing local and regional use and less on governing international spread. However, intercontinental spread of antibiotic resistance is increasingly well documented for some of the most worrying resistance genes in gram-negative pathogens, which are reported as endemic in a growing set of countries (Figure 2C) [22]. Although there are still few reports of intercontinental spread of insecticide and herbicide resistance, common exchange of plant and insect pests among continents similarly imperils pesticide susceptibility (see [22] for examples).

Priorities for Coevolutionary Governance
Priorities for governing coevolution can be derived from analysing the structure of selection and connectivity in human–environment systems. Here we focus on the overarching challenge of shifting away from the escalating coevolutionary dynamics of alternating increases in biocide use and biocide resistance. We propose three priorities for shifting cultural evolution toward achieving that goal (Figure 1B). The first is to promote cultural evolution of mental models and social norms that reduce unnecessary biocide use. The second is to diversify practices to reduce directional selection on the basis of systematic evaluation of new technology as well as principles underlying past practices. The third priority is promoting collective action to govern connectivity from the local to the global scale, which will help reduce the spread of resistance. A range of case studies illustrate the implementation of these priorities for biocide resistance in the context of production systems and health systems (Figure S1 in the supplemental information online).

Priority 1: Shifting Mental Models and Social Norms
Mental models and social norms play an important role in determining which solutions are applied to a problem [29,30] and can become engrained as part of emergent world views or ideologies [31]. Norms are embedded in cultural and historical contexts, underpin legal systems of action, can evolve with changing conditions, and may arise around novel opportunities such as those afforded by new technologies. The multigenerational state shifts in practice brought about by industrially produced biocides and transgenic crops can make agricultural communities and broader society more likely to assume that new pesticide technologies will continue to replace current ones, should widespread resistance become a problem [32]. The importance of this change in perception is supported by modelling showing that the time horizon of farmers is important for how likely they are to implement resistance management strategies [33,34]. To shift these evolving perspectives, initiatives to lower excess antibiotic prescribing illustrate that social norm feedback, including from authorities and peers, can substantially reduce antibiotic prescribing at low cost and on a national scale [35,36].
Priority 2: Systematically Diversifying Practices
Evaluating opportunities for integration of new as well as old technologies and practices is a priority for meeting the challenge of systematic diversification. Although focus is often on new technological opportunities, the advances of modern medicine and agriculture can sometimes lead us to forget the practices of the past that, in combination with new technological capabilities and scientific insights, can help build critical resilience [10]. Signs of systematic prioritisation of diversity are emerging. The diversity provided by some experienced-based practices in agriculture was adopted under the name of IPM in the middle of the 20th century (Figure S1A in the supplemental information online). IPM can help reduce pesticide use (Figure S1A1 in the supplemental information online) and is often mandated in industrialised agriculture to reduce resistance as well as pesticide health risks [24] (Figure S1A5 in the supplemental information online). Especially for transgenic Bt crops but also for other insecticides, the old tradition of planting refuges where insecticides are not used has been key to slowing resistance evolution [21].

Likewise, in human health, recent events associated with antibiotic use have necessitated re-evaluating established practices. For example, the origin of the important antimarial drug artemisinin in Chinese traditional medicine demonstrates the value of historical uses for expanding the repertoire of current medicines [37]. More broadly, our rapidly developing knowledge and technological expertise give reason for reconsidering opportunities for mastering practices beyond pharmacotherapy, practices that once were considered unsafe and undesirable. A rapidly shifting perspective in Western medicine is in the understanding of the multiple and complex roles of microorganisms in human–microbe interactions and the risk that antibiotics disrupt these symbioses [38]. Microorganisms are increasingly recognised as a contribution rather than principally as a threat to human health. Resistant coinfections of virulent new strains of Clostridioides difficile (formerly Clostridium difficile) in patients previously treated with antibiotics infect 450,000 and are involved in 30,000 deaths in the USA annually [39]. These infections can be treated with faecal transplants that restore the gut microbiome to a healthy state (Figure S2 in the supplemental information online).

Priority 3: Collective Action for Governing Connectivity
Decisions about whether to use a pesticide or administer an antibiotic tend to be taken in consultation with crop consultants and fellow farmers or with doctors and family, respectively. There is increasing evidence that trust, participation, coordination, and regulation are important for effective resistance management. For instance, high levels of competition can undermine trust between doctors and patients and lead to antibiotic overprescribing in areas of the USA with high densities of health care providers [40] (Figure S1B1 in the supplemental information online). Building trust through engagement and local monitoring may help overcome perceived barriers of collective action in the adoption of IPM (Figure S1A1–A4 in the supplemental information online). At the regional or national level, taxing particularly harmful pesticides can help lower their use and encourage IPM (Figure S1A5 in the supplemental information online). Similarly, the regulation and monitoring of non-Bt refuge requirements in the USA and Australia have been important for these countries’ relative success compared with countries such as Brazil and India, where resistance has evolved rapidly [21]. The potential international significance of such decisions is illustrated by the recently documented intercontinental transfer of insect pests that could be carrying insecticide resistance genes [22].

As the global spread of resistance increasingly undermines national efforts, the need is growing for new types of international institutions (i.e., accepted formal or informal practices) [23]. In a time of consolidated seed production, there remain opportunities for such institutions to govern
global dynamics by eliminating perverse incentives. For example, use of single-toxin and multitoxin Bt crops that share common toxins facilitates the evolution of resistance to multitoxins. Incentives for rapidly withdrawing single-toxin crops when multitoxin crops become available will help limit resistance [41]. In the absence of international legally binding instruments that regulate biocide use and harmonised surveillance, targeted interventions are of high importance. Following the international spread of plasmid-borne colistin resistance, likely from China, a diverse array of organisations engaged with the Chinese government to lobby for restricting use of colistin as a growth promoter [42]. However, for successful reduction of antibiotic use and resistance, governments need to implement their national action plans following the guidance of the World Health Organization global action plan on antimicrobial resistance (AMR) [23,43].

Coevolutionary Governance and Sustainable Development

Governance of resistance evolution occurs in a complex societal context with multiple and sometimes conflicting political agendas. Understanding these agendas can help guide the application of coevolutionary governance by identifying suitable solutions and leverage points. Sustainable development, concretised by the SDGs, illustrates these many competing ambitions. In this section, we discuss how coevolutionary governance of biocide resistance can be guided by and integrated with actions striving to achieve sustainable development. We identify two key SDGs for leveraging coevolutionary governance of biocide resistance, namely sustainable production and consumption and good health for all (Figures S3 and S4, Boxes 1 and 2).

Priority 1: Shifting Mental Models and Social Norms

A general challenge in promoting new perspectives in production and consumption is the limited knowledge we have about the implications of typical sustainable development strategies, such as agricultural intensification, on antibiotic and pesticide use [44]. These knowledge gaps mean that new perspectives will have to be promoted in the context of both increasing risks and high uncertainty. From a production perspective, a potential approach to reducing antibiotic use and pesticide use while contributing to sustainable development is to use ecological intensification strategies [45] that promote regulating and provisioning ecosystem services, such as biological control in crop agriculture and microbially enhanced immunocompetency in livestock [22]. For consumers, one dominant perspective that reinforces excessive antibiotic use is the norm of wasteful and meat-heavy diets [26,44]. For pesticide use, prevailing norms about the aesthetic appearance of fruit and vegetables in retail necessitates higher amounts of pesticides or other environmentally intensive means of production and storage [46].

In human health, improved basic hygiene and sanitation go a long way toward reducing the incidence of bacterial infections (Figure S3 in the supplemental information online), but new research funding is disproportionately directed to innovation of therapeutics [47]. From 1990 to 2015, the number of countries with more than 90% of the population having access to improved drinking water and sanitation increased by approximately 50% [48]. Yet, at the global level, 946 million people still defecate in the open, and 9% of the global population lack access to safe drinking water, emphasising the importance of a continued focus on improved water, sanitation, and hygiene [48].

Priority 2: Systematically Diversifying Practices

The successful promotion of the above perspectives relies on the implementation of a diversity of practices in production and consumption, as well as in health systems. In production, beyond the promotion of IPM in crop production, aquaculture is a tremendously diverse practice that can provide alternative and potentially more sustainable protein sources [49]. However, aquaculture
Antibiotics are widely used for both human health and food production, and antibiotic resistance therefore epitomises the challenge of governing coevolution in the context of interlinked sustainable development goals [5,43] (Figure S3 in the supplemental information online). Because we are unlikely to see new and widely available classes of antibiotics on the market before 2030, we must preserve susceptibility to current antibiotics [22,23,38]. Succeeding with this goal is an enormous challenge because the demand for antibiotics for both animals and humans is projected to increase drastically under business-as-usual conditions [25,26].

The main opportunities for decreasing antibiotic use for humans through sustainable development are (i) improving hygiene and sanitation to reduce infection rates, (ii) changing health systems to improve treatment and prevention, and (iii) reducing poverty. Infectious diseases are among the largest contributors to global mortality rates, especially among children, and therefore one of the greatest challenges to achieving the goal of universal good health [1,5,18,43]. Treatment of infectious diseases accounts for a large proportion of global antibiotic use; yet, insights about how global progress in preventing infectious diseases translates to reductions in antibiotic use are hampered by lack of monitoring of the latter. With regard to sanitation, antibiotics are used to treat an estimated 494 million diarrhoea cases annually just in Nigeria, India, Indonesia, and Brazil, and unless the sanitation infrastructure is improved by 2030, this number is estimated to increase to 622 million [18]. Providing universal access to improved water and sanitation in these countries could reduce the volume of prescribed antibiotics by 60% [18]. The pressing need for improved access to universal health care (UHC) is illustrated by the fact that a minimum of 50% of the world’s population lack full coverage of essential health services [53]. In this process of providing UHC, it is important to consider the economic structure of health systems to reduce poverty and facilitate sustainable use of antibiotics. Finally, the two main opportunities to decrease antibiotic use in food production are (i) dietary change toward reduced meat consumption and redistribution of the resources used to produce animal protein, which will help improve food security and reduce hunger; and (ii) sustainable ecological intensification of production systems, which will help address climate change, biodiversity loss, and land and ocean degradation [22,26].

At the consumer level, the potential for reducing biocide use and other environmental harms through purchasing of quality, local, or in-season products depends on context [50,51]. Organic

**Box 1. Antibiotic Resistance and Sustainable Development**

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**Box 2. Pesticide Resistance and Sustainable Development**

Compared with antibiotic resistance, resistance to insecticidal and herbicidal pesticides exhibit more limited gene exchange between human health and production systems. Pesticide use mainly takes place in crop production and consumption with complementary uses in domestic and industrial pest control and human health (especially for vector control). With projected increases in global population and national economies, pesticide use will likely increase in the future, although no formal projections have been attempted as they have for antibiotics. Many analyses often assume that food production must intensify to feed a growing and wealthier population but are vague on the means through which this intensification will take place [44]. Whether such increases in yield take place through increases in agricultural inputs, such as pesticides, or through intensification of agroecological management practices will have great impacts on pesticide resistance and ultimately on the sustainability and plausibility of these scenarios [60].

The main opportunities for reducing and improving pesticide use are through change in consumption and production patterns (Figure S4 in the supplemental information online). Ecologically sustainable intensification can help reduce pesticide use, biodiversity loss, climate change, and land and water degradation while improving food security and reducing hunger [44,49]. The main opportunities for improving pesticide use through sustainable development is reducing poverty, which will improve farmer capacity to reduce pesticide misuse and consumer capacity to buy products with low and less harmful pesticide use. Evidence suggests that a significant proportion of pesticide use could be removed to the benefit of farmers, consumers, and society in general, especially in low- and middle-income countries, but also without compromising yields among producers in some large, high-income countries [51]. For example, 78% of pesticide use in Thailand was described as unnecessary overuse from both a private and societal perspective [62]. Studies in the Philippines and Ecuador estimated that reduced pesticide use could lessen acute health problems, increase labour productivity, and increase farm profits [63,64]. In Africa and Asia, wider adoption of integrated pest management resulted in a yield increase of 40% and a 30% decline in pesticide use, suggesting that at least 50% of pesticide use was not needed in many agroecosystems [53].
products, for example, tend to have lower antibiotic use than conventional production forms as well as lower prevalence of multiresistant bacteria (in meat) and pesticide residues (in produce), with one estimate of 30% overall risk reduction [50,51].

In human health, effective health systems use a diversity of strategies in the pursuit of limiting antibiotic misuse. Access to such systems through universal health coverage (UHC) can reduce mortality, limit the incentives for self-medication, and reduce unregulated sales of antibiotics (Figure S3 in the supplemental information online). UHC can improve access to a range of key services, such as vaccines, with 11.4 million annual antibiotic days per year potentially avoided in children younger than 5 years of age through universal coverage with the pneumococcal conjugate vaccine [19].

Priority 3: Collective Action for Governing Connectivity
Institutions for collective action are needed to realise a number of synergies for decreased biocide use and the SDGs. Promising examples of where IPM implementation on an areawide, collective basis has succeeded and where individual, farm-by-farm approaches have previously failed could help overcome persistent obstacles to further IPM adoption [52]. Additionally, large-scale training of millions of smallholder farmers have proved successful in enhancing yields and lowering nutrient-related environmental pressures with 10–15% without increasing pesticide use [53].

Collective action is also key to the pursuit of providing UHC while reducing antibiotic misuse as out-of-pocket health expenses push close to 100 million people into extreme poverty every year [54] (Figures S3 and S4). For example, the median overall cost of treating sepsis caused by resistant pathogens in India corresponds to 442 days of wages earned by a rural male worker [55]. These out-of-pocket expenditures are strongly correlated with resistance in LMICs, likely because patients are pushed into the less well-regulated private sector to purchase medicines [56]. Finally, with slow political progress in limiting antibiotic use in animal production, alternative collective action strategies are needed. Here, pressure from consumer groups has pushed some fast-food restaurants to increase transparency about meat sourcing in relation to antibiotic use [23].

Concluding Remarks
Understanding how human cultures and living environments coevolve provides key leverage points for governance toward sustainability. Because biocide resistance is a challenge characterised by tightly coupled coevolutionary dynamics, it can also inform the way society faces other problems where ungoverned environmental change risks undermining sustainable development (see Outstanding Questions). For such benefits to materialise, online learning platforms for empirically studying and synthesising evidence on the social-ecological dynamics of biocide resistance and other environmental challenges will be important because they can provide distributed mechanisms for uptake of new insights. Such platforms will also be able to inform much-needed consolidated science policy interfaces, such as the proposed independent panel on evidence on AMR, which would allow for an integrated coevolutionary approach to inform lasting global governance mechanisms.

Author Contributions
P.S.J. conceived of the manuscript on the basis of discussion with all coauthors. P.S.J., C.F., K.M., P.J.G.H., M.T., and A.Z. wrote the first draft of the manuscript with subsequent contributions from all coauthors. All data are available via the references cited in the article.
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