Supplementary materials for "The Anthropocene and the biodiversity crisis: an eco-evolutionary perspective"

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Appendix 1. Climate change and its impact on biodiversity

Climate change is presented (too) briefly in section II of the main text, and then serves as the avatar of global change upon which I developed the overshoot idea. I add here a bit of information characterizing its various aspects and impacts on biodiversity.

What is climate? It is the spatial and temporal distribution of conditions in the Earth's atmosphere, characterized by variables such as temperature, rainfall, sunshine, etc. (<u>https://en.wikipedia.org/wiki/Climate</u>). All these variables have statistical distributions, which can be characterized by means or variances, but also by extreme points—known as extreme events (e.g., hurricanes). While all these variables can vary greatly over time (e.g., from one year to the next), climate change concerns directional variations (e.g., increase) in relation to a standard. This standard is often the average pre-industrial value (i.e. around 200 years ago).

Let me recall a few values already given in the main text. The proven increase is already 1.3 °C above the pre-industrial mean value (see Schmidt, 2024) on a global scale, with Western Europe already experiencing an increase of 2.3 °C (Vautard et al., 2023). 2023 has been the hottest year ever, with 1.5 °C above the pre-industrial mean value (Schmidt, 2024), and 2024 is predicted to be even hotter. Marine heatwaves that have about doubled in frequency since the 1980s (IPCC, 2023, chapter 11; Otto, 2023), and the number of major hurricanes in the North Atlantic has at least doubled, depending on models (Emanuel, 2021). In addition to their direct

effects, climate change naturally has indirect effects on ecosystems, such as floods or forest fires on an unprecedented scale, in the general context of a massive disruption of bio-geochemical cycles.

Variables such as temperature are fundamental to life, and therefore to ecological and evolutionary processes. Climate change will therefore affect biodiversity via the metabolisms (e.g., molecular, physiological) of living organisms, since they closely depend on, for example, temperature. The effect will then spread to all levels of biodiversity (Figure 2), affecting the interactions between living beings or their interactions with the abiotic environment. This effect has been the subject of a considerable number of studies. Even if it is not the main cause of species extinction, the IPBES estimates that 5 to 15 % of species are at risk of extinction under a warming scenario of between +2 °C and +4.3 °C (IPBES, 2019). Let us have a closer look at two examples involving key aspects of eco-evolutionary dynamics:

- For organisms living in the temperate zones of the Northern hemisphere, climate change induces earlier favorable conditions for the "start of life" in spring, such as tree bud burst or reproduction in animals. Studies carried out on blue tits (*Cyanistes caeruleus*) in evergreen forests in the south of France have shown that reproduction (egg laying) starts around ten days earlier, corresponding to an earlier peak in food availability (caterpillars; Bonamour et al., 2019). This response to climate change seems to be based on phenotypic plasticity, but we have the beginnings of an eco-evolutionary loop in the interaction between blue tits, caterpillars, and presumably trees (caterpillars are feeding on leaves). Note, though, that such a response has not been observed in deciduous forests despite similar trends in climate change (Bonamour et al., 2019), highlighting that responses may differ with local conditions.
- In addition to the temporal shift in favorable environmental conditions, climate change induces a spatial shift. The distributions of one half of terrestrial flightless mammals and one quarter of threatened birds may indeed have been negatively impacted by climate change (IPBES, 2019). Species are indeed tracking favorable (see Box 2): for example temperate species are moving towards the poles, leading to rapid changes in distribution ranges. Chen et al. (2011) show, for example, a northward shift in Europe of almost 2 km per year over the last 30 years, with marked variation between species. Blowes et al. (2019) highlight another aspect: a significant turnover of local species assemblages on a global scale. This leads to new species-species and species-environment interactions, a cradle for new eco-evolutionary dynamics.

Appendix 2. Temporal trends in human-induced impacts (stressors) on biodiversity and the overshoot effect.

We use here the idea of an "overshoot period" (Meyer et al., 2022), developed in the main text for temperature (climate change), arguing that it could be a useful framework for other major stressors of biodiversity, i.e. (i) land/sea appropriation (fragmentation and use) and (ii) invasive alien species. An increase in temperature is a global phenomenon, with, of course, local variation, which is not necessarily the case for the other stressors. However, the overshoot framework can account for a variety of spatial scales, and can, therefore, be useful for analyzing the stressor impact, but also to derive predictions and to build and implement solutions.

In this framework, stressor effects are estimated using variables, the value of which varies in time (increases or decreases depending on the variable), from a pre-industrial value to a threshold value at which the overshoot period begins (Figure 1). This period can last for varying lengths of time (e.g., decades) before returning to conditions more favorable to biodiversity, depending on the implementation of mitigation actions and their temporality (Figure 1), and even be of "infinite" length (centuries to millenials). The notion of overshoot makes it possible to arbitrarily fix the duration of the effect in models and scenarios, and to assess how biodiversity will respond to these new conditions in terms of eco-evolution over time. As for temperature change, the evolutionary consequences (not developed here) can be considered based on trait evolution and environmental tracking (Figure 3).

A. Land and sea appropriation (fragmentation and use)

A species occupies space according to its ecology (e.g., ecological preferences, interactions with other species and the environment) and its evolutionary background (e.g., adaptive radiation, extinction rate), including deterministic and stochastic processes for both aspects—all this results in a distribution area, which is occupied more or less continuously by populations of that species. Whether the distribution is continuous or discontinuous, migration ensures the genetic and demographic connection between populations, which requires migration corridors (in the broadest sense). We can also reason at the level of communities of species that occupy common sites, and migration also plays a connector role. The reader is referred to general references for detailed explanations on these processes, from the population to the ecosystem level (Futuyma and Kirkpatrick, 2018; Leibold and Chase, 2018; Loreau, 2010; Relyea and Ricklefs, 2018).

A very marked aspect of the Anthropocene is the appropriation of space by human activities and subsequent artificialization, which leads to the encroachment on species' distribution areas, reducing them or even making them disappear (Díaz et al., 2018; Dirzo et al., 2022; Ellis, 2021; Solé and Levin, 2022). Urbanization and agricultural/aquaculture activities are good examples. Solé & Levin (2022) highlight that "crops, settlements and forestry already cover 57 % of emerged lands". Moreover, 70 % of the Earth's land surface potentially occupied by plants has been altered (IPBES, 2019). The reduction in the biomass of terrestrial vegetation has been halved (Erb et al., 2018), with an estimated loss of approximately 20 % of its original biodiversity (Díaz et al., 2018), since the onset of agriculture. It should be noted that this appropriation is of course physical (e.g., construction of urban spaces that are

highly unfavorable to biodiversity), but also sonic, olfactory/chemical, or visual... we therefore have a general fragmentation of the living landscapes of populations, species and communities, and therefore a profound alteration of their ecological functioning and evolution. It is difficult to evaluate when it will stop on a global scale, because it depends on many factors (e.g., population size of humans and their commensals, intensity of mitigation actions). Even if the size of the world's human population stabilizes (e.g., by 2050), it is even likely that this appropriation will continue, particularly with increasing (peri)urbanization (James and Douglas, 2024; Szulkin et al., 2020), more land dedicated to agriculture (Solé and Levin, 2022), and more intensive use of the oceans (Jouffray et al., 2020; Pauly and Jacquet, 2019).

The effect of stressors is represented in Figure S1 for urban and agricultural space use, as in Figure 1 from the main text for temperature, allowing to contrast two hypothetical situations. For urban space use (Figure S1 top), the stressor effect increases with time, and then reaches a plateau—in practice, it is difficult to predict if and when a plateau will be reached. However, it seems likely that the overshoot effect will be quite strong (and long), as human deartificialization will be complicated to implement. For example, it is hard to see how large-scale urban de-artificialization could take place, given the phenomenal quantities of concrete and other materials used in the urbanization process. [It is difficult to find relevant scientific references for concrete production, but https://www.sustainabilitybynumbers.com/p/china-uscement suggests an annual cement production of ca. 4 * 10⁹ T/yr, i.e., 500 kg/human being. As the surface of emerged lands is ca. 150 million km² and three tons of cement have a volume of 1 m³, and assuming that the total production of cement in human history has been 100 times the current annual value, we get a 1-mm crust over all continents. Note that cement contributes to ca. 5 % of greenhouse gases emission]. Even if human activities were to vanish instantly, the return to a quasi-ecological equilibrium would take millennia, involving erosion by climatological and meteorological forces. A further difficulty will be to define overshoot value at the Earth's scale—a simple variable, such as temperature, is not an option. It would therefore be necessary to adopt a set of objectives, similar, for example, to the approach used to define the sustainable development goals (https://sdgs.un.org/goals), and therefore possibly several overshoots. The situation might be less gloomy for agricultural land use (and fisheries), as reaching a plateau in surface used is possible through various ways (e.g., decreasing meat / fish consumption; Godfray et al., 2018) and even perhaps to come back to pre-overshoot conditions (Figure S1 bottom).

Of course, areas occupied or used by humans are not devoid of biodiversity, even if it may be greatly reduced, in terms of e.g. number of species (per unit area), number of individuals per species, or ecological complexity (James and Douglas, 2024; Szulkin et al., 2020). Some species also have "specialized" in these areas—they can be broadly considered as "invasive species", some of which have taken advantage of agricultural areas (see e.g. Radosevich et al., 2007; see also section B below). Whether invasive or not, these species have adopted new ecological niches, thus seeking new ecological and evolutionary optima. Moreover, we know that populations are adapting fast to anthropized environments (e.g., Chen et al., 2023; Szulkin et al., 2020), sometimes at a cost of decreased fitness or trait evolution.



Figure S1A. Time curves of consequences of human activities, past and future (modified from Meyer et al., 2022). This is Figure 1 (main text) customized for space use (top: urban areas, and bottom: surface devoted to agriculture). The present is indicated by "Present".

Top figure. Urban areas have tripled over the last three decades - 0.22 to 0.69 % of the Earth's land area, based on artificial night-time light (Zhao et al., 2022). Depending on the way urban areas are defined, values of up to 3 % can be obtained (Liu et al., 2014), and it is therefore hard to evaluate how the current value scales with pre-industrial values, but an order of magnitude is not unlikely. Let us retain the 0.69 % value, and assume a 1 % target for the beginning of the overshoot period, and a plateau at 1.5 % (as an optimistic prediction). We kept the dotted line only, which represents the most likely situation, since de-urbanization on a large spatial scale seems unlikely, with therefore a very long overshoot period. Biodiversity should therefore adapt, ecologically and evolutionary, to these urban conditions.

Bottom figure. The Earth's surface dedicated to agriculture (as of 2019) is one third of the land surface (FAO, 2021). Let us assume a 40 % target for the beginning of the overshoot period, and a plateau at 45 %. Here we assume that because of improvements in agricultural production and consumption (e.g., less food waste) the plateau will last for a few decades before decreasing—this is arguably optimistic, but perhaps less optimistic than the plateau assumed for urbanization. If agricultural surfaces indeed decrease, biodiversity will have to re-adapt to previous conditions (situation B in Figure 1). Similar figures can be drawn for among others forestry, fisheries, and road, air and sea traffic.

An example is a reduction in adult size in fish species as the result of fishing pressure via the mesh size of fishing nets (Heino et al., 2015; Pauly and Jacquet, 2019). For urbanization, the overshoot plateau could last a long time (Figure S1 top), and the impact of adaptive evolution could be more marked than for climate change (situation B in Figure 3 from the main text). Of course, this possibility of adaptive evolution and tracking of evolutionary optima will

depend on population size—a small size, which is not unlikely in such an environment, would be unfavorable, with a more marked role for genetic drift and slower adaptation. In the example of land use for agriculture as considered here (Figure S1 bottom), there will be less time for adaptive evolution than for urban space, and we are back to the situation considered in the main text for climate change (Figure 3).

The above reasoning has been carried out on a global scale, but it can be adopted on a regional or even local scale. Urban de-artificialization could serve as an example, based on policies defining locally a maximum level of urbanization, or even de-urbanization in favor of spaces more favorable to biodiversity (e.g., urban parks; Beninde et al., 2015; Chen et al., 2023). On this scale, it seems possible to assess the ecological and evolutionary forces at work. In practice, many urban communities have set up de-artificialization plans with quantified targets. The overshoot grid could be a useful tool for defining these objectives. It remains unclear whether actual eco-evolutionary loops/feedbacks have been set up beyond a very local scale, i.e. whether species occupying urban space are evolving in such a way to modify their environment, driving further evolution (Chen et al., 2023; Szulkin et al., 2020).

B. Bioinvasions

Bioinvasions are defined as the occurrence of a species outside its range, a process that involves active or passive migration of individuals from their origin environment (Williamson, 1996; Davis, 2009; Simberloff, 2013). This is a natural process, which enables the colonization of new environments, such as volcanic islands, once they have risen (see e.g., Whittaker et al., 2023). We are considering here bioinvasions linked to human activities—a species becomes an invasive alien species when it extends its distribution, post-introduction, via positive demographic growth (Williamson, 1996; Davis, 2009). In fact, since the first colonizations (e.g., out of Africa), humans have allowed/induced biological invasions (Ellis, 2021, 2015), but these have taken on a more significant scale with the massive development of long-distance travel, and the transport of cash crops or amenity species to acclimatize and use them outside their original range (Williamson, 1996; Davis, 2009; Ricciardi et al., 2013; Jeschke and Heger, 2018; Simberloff, 2013), possibly through human assistance (Brodie et al., 2021; Ricciardi and Simberloff, 2021). The invasion process is often characterized by different phases of varying duration—for example, there is often a waiting period after initial colonization, before rapid exponential growth, often followed by a decline (Figure S1B).

The whole process can be extremely rapid, with the possibility of a large-scale geographic spread taking no more than a few years (e.g. zebra mussel in North America, Karatayev and COVID-19 Burlakova, 2022)—the spread is an even better example (https://en.wikipedia.org/wiki/COVID-19 pandemic). Both because of this rapid growth and the fact that the number of invasive alien species continues to rise (Seebens et al., 2017), these species play a major role in biodiversity dynamics, being a major source of imbalance for local species, communities and ecosystems because they may outperform local species of the same ecological guilds (Davis, 2009; Ricciardi et al., 2013; Simberloff, 2013; Williamson, 1996). Predator invasive alien species have a more direct impact on native species through consumption. Invasive alien species are indeed considered to be a major source of biodiversity loss and of disruption of Nature's contribution to people (Diaz and Malhi, 2022)-probably the leading cause of species extinction through predation (David et al., 2017; Roy et al., 2024). In

addition, they have significant socio-economic impacts, for example costing the global economy billions of dollars (Cuthbert et al., 2021; Diagne et al., 2021).



Figure S1B. Temporal dynamics of an invasive species. "Number" (y-axis) can be, for example, the number of individuals in a site, or the number of occupied sites in a landscape. The curve on the left represents an "idealized" dynamic, consisting of a waiting phase (1), followed by exponential growth (2) and no less rapid decline (3) to reach a plateau of variable value (4). In this situation, a single mode separates growth and decline. In real situations (right-hand curve), a more complex dynamic is more likely, with numerous phases of growth and decline.

Biological invasions are therefore a good candidate for an overshoot-type representation (as in Figure 1 from the main text, and Figure S1A). However, as they are constantly increasing and the process concerns all environments and biological groups, it is difficult to predict when a plateau will be reached (Figure S1C). We can, however, set a plateau target, based on quantified objectives, including values that should not be exceeded (for example, +30 % invasive alien species), an ecological cost (e.g., the number of species disappearing because of invasions), a value of biodiversity homogenization (communities are less different than they were before the spread of invasive alien species; Roy et al., 2024), or an economic cost (Cuthbert et al., 2021; Diagne et al., 2021). Estimating these values (the number of invasive alien species in the future, or their ecological cost) might require complicated modeling exercises with a lot of uncertainties.

Note that the future dynamics of invasive alien species may interact synergistically with space appropriation (see section A). Newly artificialized habitats are excellent environments for the most opportunistic invasive alien species (see e.g., the list of the 100 most aggressive invasive species;

https://en.wikipedia.org/wiki/100_of_the_World%27s_Worst_Invasive_Alien_Species). Colonizing such habitats might not have an impact in terms of numbers of invasive species, since these species are already invasive, but certainly in terms of fauna homogenization on various geographical scales.



Figure S1C. Time curve of consequences of human activities, past and future (modified from Meyer et al., 2022). This is Figure 1 (main text) customized for invasive alien species on a global scale. The present is indicated by "Present". The number of invasive alien species is estimated to be at least 37,000 (Roy et al., 2024), and we assume that this represents 70 % of the target value not to be trespassed—this is extremely difficult to predict, but compatible with current dynamics (Seebens et al., 2017). As (i) a major fraction of invasive alien species will not come back to a status of "non invasive" and (ii) these species are extremely difficult to extirpate, the overshoot period is likely to be extremely long. Considering a more local scale may produce a less gloomy picture, since points (i) and (ii) are not necessarily true.

Appendix 3. Some winners and forgotten ones in the biodiversity crisis.

Winners

Invasive alien species have largely benefitted from human activities and the growth of the human population and contributed to the biodiversity crisis (Appendix 1B). Examples we think less about in this crisis are "commensals"/"domesticates" (i.e., food, pets, parasites, microorganisms), which corresponds to a rather low number of species, for example less than 50 among animals. However, their biomass far surpasses that of wild species—for example, the biomass of livestock (≈ 0.1 Gt C) is estimated to be more than 100 times that of wild mammals (≈ 0.007 Gt C; Bar-On et al., 2018). The benefits for these species are manifold, including demographic growth, a wider distribution area, and new ecological conditions. Both commensals and invasive alien species have reached (can reach) numbers that are at least three orders of magnitude higher than expected for similar organisms at the same levels in trophic chains. For example, cats and dogs are counted in billions at Earth's scale, while the population size of such predators should not exceed (tens of) millions.

Commensals and invasive alien species are also those that have benefitted the most from another impressive result of human activities, namely biodiversity hauling and enlargement of distribution area (Davis, 2009; Williamson, 1996). Commensals (again cats and dogs, but also rats or crops) can now be ubiquitous—crops are good examples with generally located origins (e.g., corn in Central America, now cultivated over 2 million km²). Both the increase in numbers and biodiversity hauling strongly impact(ed) biodiversity, directly through, for example, predation by invasive alien species, which is the primary source of local species extirpation (David et al. 2017). Indirect effects might result from the agro-industrial production, and associated land/sea use, required to feed pets or livestock—for example, grazing land makes up 30 million km² (<u>https://ourworldindata.org/global-land-for-agriculture</u>; 20 % of emerged lands).

Note that biodiversity hauling can also result from global change itself (Pecl et al., 2017)—again the most popular example is climate change, with species poleward migration to colonize areas that were previously unfavorable (see main text). New areas are colonized, and new ecological niches occupied, with major and cascading effects on ecosystems and even on the climate (Davis, 2009; Ellis, 2015; Meyer et al., 2022; Solé and Levin, 2022). The ecological extinction of declining species is therefore (more than) matched by the ecological colonization of these growing species.

Forgotten ones? Are bacteria at risk as any other species?

Bacteria form the starting point of biodiversity, having been the first living organisms on the Earth's surface, perhaps over four billion years ago (Judson, 2017; Lynch, 2024). They make up the bulk of biodiversity, even if the number of species remains poorly known: 10,000 species have been described, and the estimates of a few tens of thousands of species from a few decades ago (Staley, 1997) might be rightly downwardly biased by two orders of magnitude (Larsen et al., 2017)—these last authors suggest a value of several billions. However, defining bacterial species is not an easy task—the concepts used in pluricellular eukaryotes, based on reproduction and sex (Coyne and Orr, 2004), can therefore hardly be used (VanInsberghe et al., 2020). Furthermore, the widely used molecular distance criteria used in eukaryotes (e.g., 97 %

homology) will tend to minimize bacterial diversity (Arevalo et al., 2019; Staley, 1997; VanInsberghe et al., 2020). If these values are true (10,000 species described out of say one billion), estimates of species loss have to be based on 0.01 % of the whole bacterial diversity. Moreover, estimating the loss of individual numbers or of intraspecific diversity is even less at hand, given that populations of most species are not easily accessible.

Answering the questions "Have we lost microbial species? Are certain species at risk because of far too low population size?" is therefore a tricky issue. The answer is probably positive (Staley, 1997), but remains to be backed by data. However, we know that environmental conditions can lead to extinctions, as has been shown in human gut microbiota with diet (Good and Rosenfeld, 2023; Sonnenburg et al., 2016), or to depressed population size as in soil bacteria with increased levels of nitrogen (Philippot et al., 2013; Wanga et al., 2018).

It might also be more relevant to consider microbes at the community level. We know that such assemblages are labile in time, and can evolve with environmental conditions—for example, such communities can be restored, compared to control conditions (Watson et al., 2022). The notion of functional landscapes to address community functions from their composition suggests that indeed community composition matters in synthetic laboratory communities, and in practice suggests a direct connection between species number and function (Skwara et al., 2023). Provided that such results can be extended to natural communities, the loss of species leads to the loss of functions, and vice versa. However, the large size often observed in bacterial populations is reinsuring: immigration from areas not exposed to toostrong impacts of the Anthropocene might provide a survival back-up for bacteria (Staley, 1997).

In the eco-evolutionary perspective proposed in this article, bacteria also represent an interesting case. The decoupling of ecology and evolution is not easy, particularly in view of the "sexual" promiscuity and fluidity between phylogenetically distant genomes due to horizontal gene transfer. As a result, it is difficult to distinguish the temporal variation of genotypes or phenotypes within a population from that of "species" in communities, and therefore what falls under evolution or ecology (Loreau et al., 2023; Martiny et al., 2015), all the more when considering bacterial communities as possible evolutionary units (Inkpen and Doolittle, 2022). This is perhaps an opportunity for the bacterial future, insofar as rapid responses, both ecological and evolutionary, to global change stressors can be put in place.

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