

4. Wurtz, R.H., and Goldberg, M.E. (1972). Activity of superior colliculus in behaving monkey. 3. Cells discharging before eye movements. *J. Neurophysiol.* **35**, 575–586.
5. May, P.J. (2006). The mammalian superior colliculus: laminar structure and connections. *Prog. Brain. Res.* **151**, 321–378.
6. Apter, J.T. (1946). Eye movements following strychninization of the superior colliculus of cats. *J. Neurophysiol.* **9**, 73–86.
7. Schiller, P.H., and Stryker, M. (1972). Single-unit recording and stimulation in superior colliculus of the alert rhesus monkey. *J. Neurophysiol.* **35**, 915–924.
8. Edwards, S.B., Ginsburgh, C.L., Henkel, C.K., and Stein, B.E. (1979). Sources of subcortical projections to the superior colliculus in the cat. *J. Comp. Neurol.* **184**, 309–329.
9. Fujimaru, Y., and Kosaka, T. (1996). The distribution of two calcium binding proteins, calbindin D-28K and parvalbumin, in the entorhinal cortex of the adult mouse. *Neurosci. Res.* **24**, 329–343.
10. Kitamura, T., Pignatelli, M., Suh, J., Kohara, K., Yoshiki, A., Abe, K., and Tonegawa, S. (2014). Island cells control temporal association memory. *Science* **343**, 896–901.
11. Ray, S., Naumann, R., Burgalossi, A., Tang, Q., Schmidt, H., and Brecht, M. (2014). Grid-layout and theta-modulation of layer 2 pyramidal neurons in medial entorhinal cortex. *Science* **343**, 891–896.
12. Donato, F., Jacobsen, R.J., Moser, M.-B., and Moser, E.I. (2017). Stellate cells drive maturation of the entorhinal-hippocampal circuit. *Science* **355**, eaai8178.
13. Witter, M.P., and Moser, E.I. (2006). Spatial representation and the architecture of the entorhinal cortex. *Trends Neurosci.* **29**, 671–678.
14. Stensola, H., Stensola, T., Solstad, T., Froland, K., Moser, M.-B., and Moser, E.I. (2012). The entorhinal grid map is discretized. *Nature* **492**, 72–78.
15. McIlwain, J.T. (1991). Distributed spatial coding in the superior colliculus: a review. *Vis. Neurosci.* **6**, 3–13.
16. Goldberg, M.E., and Wurtz, R.H. (1972). Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *J. Neurophysiol.* **35**, 560–574.
17. Muller, J.R., Philiastides, M.G., and Newsome, W.T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proc. Natl. Acad. Sci. USA* **102**, 524–529.

Evolution: Biodiversity in the Anthropocene

Erle C. Ellis

Department of Geography & Environmental Systems, University of Maryland, Baltimore County, Baltimore, MD 21250, USA

Correspondence: ece@umbc.edu

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Human influences are reshaping plant communities around the world through both extinctions and species gains. New work relating biodiversity shifts to rapid changes in climate and land use highlights the need for new biogeographic frameworks to understand evolutionary change in the Anthropocene.

For millennia, human societies have reshaped ecosystems to construct their niche — clearing land using fire, tilling soils, managing water and nutrients, and transporting, propagating, domesticating, exploiting and extirpating species [1–4]. With most of the terrestrial biosphere now transformed by human use of land and rapid changes in climate, wild habitats and wild species are disappearing at alarming rates [5]. The basic biogeophysical and biogeographical conditions under which life evolved for millions of years are being transformed by a new global force of nature distinct from any that came before [6–9]. As this planet moves ever deeper into its human age, the Anthropocene, new research is showing that the classic biogeographic frameworks used to explain the global, regional and local patterns of biodiversity and the evolutionary forces that shape them are sorely in need of updating and revision. Two new studies, both

in this issue of *Current Biology*, add to the growing body of work aiming to better understand anthropogenic changes in biodiversity (Figure 1) by relating plant species extinctions and increases in species richness to rapid changes in climate and human use of land [10,11].

Species extinctions are justifiably the most concerning of all biodiversity changes caused by humans [5]. Rates of animal extinctions are now well documented as a broad global pattern, Anthropocene Defaunation, starting with Late Pleistocene megafauna extinctions caused by overexploitation, land clearing and other environmental modifications by Late Paleolithic hunter-gatherers and continuing into the present [4]. The evidence clearly shows that major shares of faunal diversity in many taxonomic groups are on the path to extinction, with rates much higher than historical baselines [4].

The extinction record for plants is much less well documented, and rates also appear much lower, in relative terms [12]. Le Roux and colleagues' [10] detailed temporal analysis across selected biodiversity hotspots and coldspots around the world confirms these lower rates of plant extinctions over the past three centuries. Though still above predicted background rates, and therefore a matter of significant concern, plants do indeed show much lower rates of extinction than most, if not all, animal taxa, and these are also much lower than the 20% rate recently reported by the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) [5]. Plant extinctions are also characterized in great detail, in terms of diverse life forms and causes, ranging from habitat losses, agriculture and urbanization to species invasions and disturbances from hydrologic modification, mining and fire. Yet, the



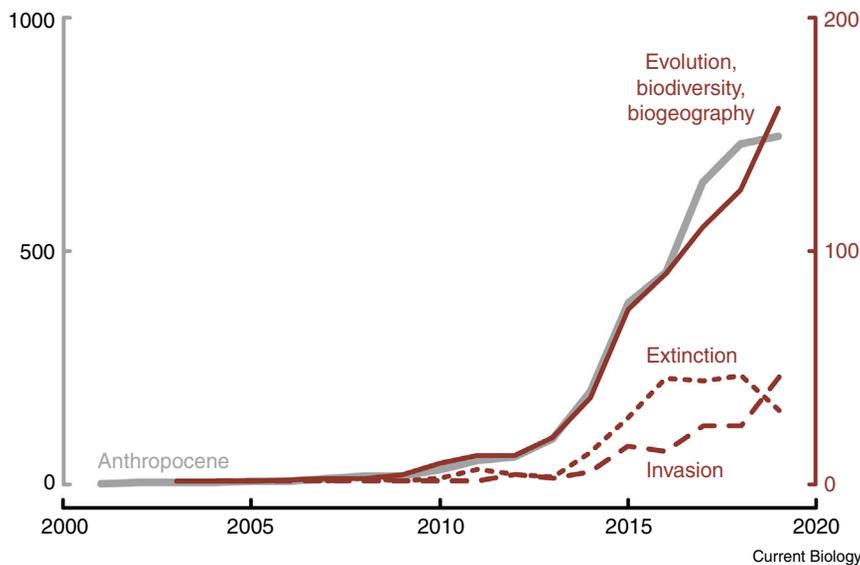


Figure 1. Published work relating to Anthropocene, evolution, biodiversity, biogeography, extinction, and invasion.

Published work relating to the Anthropocene (gray line, total of 3,123 publications) and to evolution, biodiversity or biogeography (solid red line, total of 589 publications), extinctions (short-dashed line, total of 212 publications), and invasions or invasives (long-dashed line, total of 120 publications) based on a Web of Knowledge topic search, July 18, 2019, with 2019 count adjusted for day of year.

study also demonstrates just how much remains unknown about the causes and processes of plant extinction — the cause of nearly half of all extinctions remains unknown.

More intriguing still, in contrast to the dominant environmental narrative of the Anthropocene [9], in which anthropogenic global changes are portrayed as a ‘great acceleration’ post-1950 [13], long-term rates of plant extinctions appear to have peaked before the 1950s, and to have declined significantly thereafter. As the authors and others note, data available for global and regional analyses, including this one, remain subject to geographic and other limitations in data quality and representativeness [14]. It is possible that the regions chosen for study do not represent the global patterns of change in plant biodiversity — perhaps these regions were transformed by agriculture and cities long before others, where extinction rates might now be accelerating, not declining. Still, these authors’ [10] exceptionally detailed approach to the study of plant extinctions around the world opens a new window into the biodiversity changes of the human age, showing the diversity of functional, taxonomic and causal patterns of plant extinction, while further demonstrating the need for expanded

research efforts to strengthen data availability at regional and global scales.

For good reasons, global species extinctions have tended to capture the lion’s share of popular and scientific attention relating to the Anthropocene and anthropogenic environmental change in general. Nevertheless, decades before the term Anthropocene even existed, the term Homogenocene (and Homogocene) was introduced to characterize the global scale of regional and local biotic homogenization caused by anthropogenic species transport, introductions, and invasions [9]. In particular, species invasions have long been a matter of concern, owing in part to their potential, at least in theory, to outgrow, out-reproduce, outcompete, or otherwise displace species long native to a given landscape or region, thereby causing species extirpations and even extinctions [15,16]. While causal evidence for invasion-related plant extinctions remains somewhat controversial, a number of studies have confirmed that anthropogenic species introductions and invasions have either compensated for extinctions or caused net increases in species richness at local and regional scales around the world (Figure 1) [12,15–18]. But even while the empirical basis for long-term increases in plant species richness at local and regional

scales has grown ever more robust, theoretical mechanisms explaining these biodiversity increases remain at an early stage of development. In this light, recent work by Suggitt *et al.* [11] is especially welcome.

In their analysis of plant species richness in quadrats and transects around the world, Suggitt *et al.* [11] demonstrate that local (alpha) diversity has increased the most in the coolest regions of the world. More importantly, they propose a basic mechanism to explain these changes — species increases are greater where climate changes are also greater, in absolute terms, especially in relation to changes in precipitation. Based on robust empirical work, a general theory now arises. The more local communities are ‘perturbed’ by rapid climate changes, and potentially other external geophysical or geochemical forcings, the more they will tend to experience net increases in species richness. While the generality of such a theory demands further testing, it could prove critical to understanding the increases in local and regional biodiversity that have been observed around the world in the face of the unprecedented anthropogenic global environmental changes of the Anthropocene. Assuming that these changes are allowed to continue, the general prediction of long-term increases in local plant diversity has profound implications for conservation [12,19]. No longer can a simple indicator of biodiversity, like local species richness, indicate whether or not conservation goals are being met [20], especially when it is increasingly clear that certain types of species, such as those with wider geographic ranges, are generally involved in anthropogenic species increases — not a random assortment [19].

Human societies began reshaping Earth’s global, regional and local patterns of biodiversity long before the 20th century [1–4]. A growing body of empirical work confirms that these anthropogenic changes are globally significant and ongoing at multiple spatial scales around the world. To consider these within the confines of the mid-20th century Anthropocene epoch now proposed by geologists [13] is merely to scrape the surface of a much deeper and more profound transformation of biological pattern and process confirmed by an increasing number of studies.

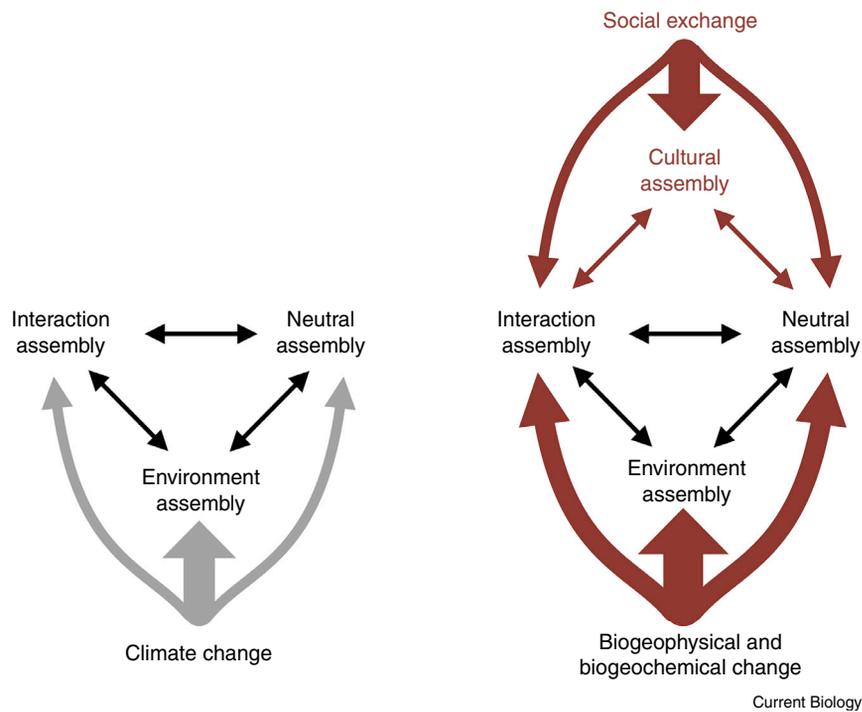


Figure 2. Processes shaping plant communities in the Anthropocene.

Processes shaping plant communities in the Anthropocene, building on the model of Jackson and Blois (left) [6]. Species interactions, environmental forcings, and neutral processes have always shaped plant communities, including the glacial–interglacial climate cycles of the Quaternary (left) [6]. In the Anthropocene, human sociocultural processes play an increasingly important role, through intentional and unintentional species transport and introductions (social exchange), through direct cultural management of species assemblages as through the propagation of favored species, agriculture and forestry (cultural assembly), and through increasingly rapid global changes in climate, soils, hydrology, nutrients, pollution and other biogeophysical and biogeochemical changes.

To better understand and potentially govern the social and cultural processes that now shape biodiversity and ecology across the increasingly human planet we live on will require improving and expanding on the classic models of community ecology, biogeography, and evolutionary processes in general (Figure 2). Accomplishing this is no minor enterprise and will demand that biologists become familiar with new forms of scientific understanding beyond their traditional training. The human societal processes that shape ecology and evolution are socially enacted, culturally defined and heterogeneous within and across societies — they are also evolving rapidly over time [1]. Nevertheless, as evidenced by the recent work presented here, the empirical and theoretical foundations are clearly being laid for a biological and evolutionary science capable of addressing the challenges of a rapidly changing anthropogenic biosphere.

REFERENCES

1. Ellis, E.C. (2015). Ecology in an anthropogenic biosphere. *Ecol. Monogr.* 85, 287–331.
2. Boivin, N.L., Zeder, M.A., Fuller, D.Q., Crowther, A., Larson, G., Erlandson, J.M., Denham, T., and Petraglia, M.D. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. *Proc. Natl. Acad. Sci. USA* 113, 6388–6396.
3. Bliege Bird, R., and Nimmo, D. (2018). Restore the lost ecological functions of people. *Nat Ecol. Evo.* 2, 1050–1052.
4. Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., and Collen, B. (2014). Defaunation in the Anthropocene. *Science* 345, 401–406.
5. Díaz, S., Settele, J., Brondízio, E., Ngo, H.T., Guèze, M., Agard, J., Arneth, A., Balvanera, P., Brauman, K., Butchart, S., et al. (2019). Summary for policymakers of the global assessment report on biodiversity and ecosystem services – unedited advance version (Bonn, Germany: Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES)).

6. Jackson, S.T., and Blois, J.L. (2015). Community ecology in a changing environment: Perspectives from the Quaternary. *Proc. Natl. Acad. Sci. USA* 112, 4915–4921.
7. Thomas, C.D. (2017). *Inheritors of the Earth: How Nature Is Thriving in an Age of Extinction* (Penguin).
8. Sullivan, A.P., Bird, D.W., and Perry, G.H. (2017). Human behaviour as a long-term ecological driver of non-human evolution. *Nat. Ecol. Evo.* 1, 0065.
9. Ellis, E.C. (2018). *Anthropocene: A Very Short Introduction*, (Oxford: Oxford University Press).
10. Le Roux, J.J., Hui, C., Castillo, M.L., Iriondo, J.M., Keet, J.H., Khapugin, A.A., Medail, F., Rejmánek, M., Theron, G., Yannelli, F.A., and Hirsch, H. (2019). Recent anthropogenic plant extinctions differ in biodiversity hotspots and coldspots. *Curr. Biol.* 29, 2912–2918.
11. Suggitt, A.J., Lister, D.G., and Thomas, C.D. (2019). Widespread effects of climate change on local plant diversity. *Curr. Biol.* 29, 2905–2911.
12. Vellend, M., Baeten, L., Becker-Scarpitta, A., Boucher-Lalonde, V., McCune, J.L., Messier, J., Myers-Smith, I.H., and Sax, D.F. (2017). Plant biodiversity change across scales during the Anthropocene. *Annu. Rev. Plant Biol.* 68, 563–586.
13. Head, M.J. (2019). Formal subdivision of the Quaternary System/Period: Present status and future directions. *Quaternary Internat.* 500, 32–51.
14. Gonzalez, A., Cardinale, B.J., Allington, G.R.H., Byrnes, J., Arthur Endsley, K., Brown, D.G., Hooper, D.U., Isbell, F., O’Connor, M.I., and Loreau, M. (2016). Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. *Ecology* 97, 1949–1960.
15. Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., De Frenne, P., Verheyen, K., and Wipf, S. (2013). Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. USA* 110, 19456–19459.
16. Sax, D.F., and Gaines, S.D. (2003). Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18, 561–566.
17. Ellis, E.C., Antill, E.C., and Kreft, H. (2012). All is not lost: plant biodiversity in the Anthropocene. *PLoS One* 7, e30535.
18. Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., and Magurran, A.E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344, 296–299.
19. Newbold, T., Hudson, L.N., Contu, S., Hill, S.L.L., Beck, J., Liu, Y., Meyer, C., Phillips, H.R.P., Scharlemann, J.P.W., and Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. *PLoS Biol.* 16, e2006841.
20. McGill, B.J., Dornelas, M., Gotelli, N.J., and Magurran, A.E. (2015). Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol. Evol.* 30, 104–113.