

Historical land use patterns provide insight into contemporary insect diversity loss

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Healthy insect populations are vital for maintaining natural ecosystems and essential to global food security. The ongoing dramatic loss of insect species and biomass is thus a global cause for concern, with much focus on this topic in the media. Yet, determining the mechanism behind these declines remains difficult, particularly when attempting to differentiate between anthropogenic drivers of biodiversity loss and long-term natural fluctuations. In a From the Cover manuscript in this issue of *Molecular Ecology*, Crossley et al. (2022) examined the long-term impact of land use change on freshwater insects by estimating levels of genetic diversity with publicly available data for the cytochrome c oxidase subunit 1 (CO1) mitochondrial locus from >700 aquatic insect species across the United States. Contemporary genetic diversity measures reflect both current and past demography and therefore are related to both past and present habitat change. Crossley et al. found that environments with greater cropland extent over the last 200 years were associated with lower genetic diversity in contemporary aquatic insect populations. This indicates that historical land use is an important factor in contemporary population dynamics. Most critically, in regions of historical cropland cover that have been converted towards other uses (such as urban environments) more recently, aquatic insect populations exhibited higher levels of genetic diversity, indicating a possible rebound in insect populations after cessation of agricultural activity. This study highlights the power of using publicly available data to answer crucial questions regarding the current biospheric emergency.

While insect population declines and biodiversity loss has been a source of major concern in recent years, research has been inconclusive regarding the extent of the decline and its ultimate cause. Indeed, recent research has indicated that while terrestrial insect populations have declined on average 9% per decade, aquatic insects have *increased* ~11% per decade (Van Klink et al., 2020). The discrepancies in research outputs may be caused by increases in taxonomic and ecological knowledge of aquatic insects resulting in increased or improved surveying efforts artificially resulting in demographic increases (Barbosa et al., 2013), a reliance on measures such as total biomass or overall insect abundance, or failure

to incorporate long-term trends in anthropogenic impacts (Crossley et al., 2022; Jähnig et al., 2020). One way in which to mediate some of the problems associated with traditional ecological abundance surveys is to assess measures of genetic diversity, which are somewhat robust to sampling strategy and provide a powerful reflection of population size and adaptive capacity.

In this study, Crossley et al. looked at the genetic diversity of >700 insect species to assess the impact of historical land use change. They focused on species that fall into the Ephemeroptera, Plecoptera, and Trichoptera (EPT) index of stream water quality (Lenat & Penrose, 1996) comprising mayflies, stoneflies, and

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caddisflies (see Figure 1). EPT species are known to be relatively intolerant of commonly-used pesticides found in agricultural runoff, thus their population health is intrinsically linked to agriculture. Using a total of 11,298 sequences comprising 1974 populations across 717 species, Crossley et al. estimated nucleotide diversity for each population within a 1 km radius—a conservative range-size estimate to minimize diversity inflation due to migration and sampling from multiple populations at once. Comparing the observed spatial patterns in genetic diversity to data on land use change from the US Department of Agriculture (USDA) Census of Agriculture (see Figure 1), Crossley et al. found that, while contemporary cropland extent was clearly linked with reduced genetic diversity, the regions with the lowest genetic diversity in insects were those that had high pre-1950s cropland extent. Given the dramatic changes in spatial distribution of US cropland cover in the 1950s and the advent of industrial agriculture post-WWII, this result was surprising. It indicates that a higher extent of cropland cover negatively impacted insect populations even in the absence of modern agrochemical pollution.

Crossley et al. used only publicly available data for their study, illustrating ways in which public repositories can be creatively used to answer crucial questions in our current biospheric emergency. Their sequence data are sourced from hundreds of previous studies dating from the 1980s until recent years, although Crossley et al. state

that the majority of the sequences are from the last decade. While using genetic data at this scale does come with limitations (e.g., differences in sampling and sequencing regimes, possible batch effects, differences in sampling year), sourcing large datasets from public repositories is one of the most cost-effective ways of accessing data for metagenetic studies (Leigh et al., 2021). These genetic data were all from the cytochrome c oxidase subunit 1 (CO1) locus on the mitochondrial genome. Nuclear or whole-genome data often provides more accurate estimates of intraspecific genome-wide variation than mitochondrial sequences, which are subject to the effects of maternal inheritance and higher rates of non-neutral evolution than nuclear DNA data (Leigh et al., 2021). Yet, nuclear sequences are far less likely to be publicly available, particularly for insect species across a broad geographic range, due to their cost and relative novelty. Thus, while not necessarily an ideal locus for assessing genetic diversity, there are several advantages to the CO1 locus. First, its high interspecies variability and accessibility for thousands of species has made this sequence a popular choice in metabarcoding studies (see Deagle et al., 2014). Second, interspecific differences occur over relatively short fragments (<500bp) and, as it is part of the mitochondrial genome, each cell retains multiple sequence copies making CO1 easy to amplify, even within degraded or mixed species samples (e.g., eDNA of water samples or animal faeces) (Deagle et al., 2014).

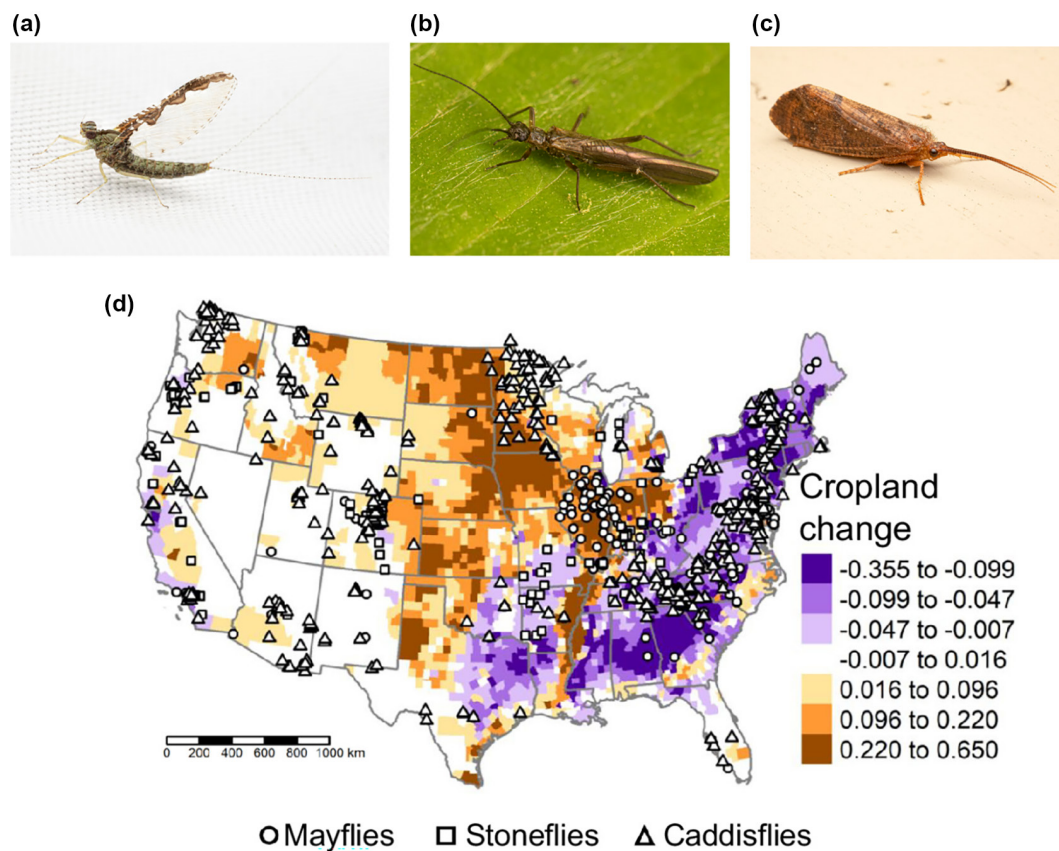


FIGURE 1 Aquatic insects and land use change. Three aquatic insects falling into the EPT water-quality index are here shown: (a) Mayfly, (b) Stonefly, and (c) Caddisfly. Photos by Solomon Hendrix. (d) Difference in average cropland cover pre- and post-1950 and sampling locations for each order. Figure from Crossley et al. (2022).

While broad spatial patterns of genetic diversity were observed by Crossley et al., the exact mechanisms driving these patterns are still to be determined. Future work could focus on understanding the mechanistic relationship between long-term cropland cover and declines in aquatic insect genetic diversity, as insight into this may be vital for preventing future declines. Mechanistic insights can likely be drawn from reviewing changes in technological and agrochemical practices over the past 200 years and how these subsequently lead to intensification and an increase in negative, often polluting, impacts to neighbouring waterways. In standard agricultural practices, large quantities of agrochemicals, biological material, residual drugs, sediments, and saline are often discharged into neighbouring aquatic habitats, negatively affecting insect communities (Mateo-Sagasta et al., 2017). However, the threshold at which a shift in agricultural practices results in insect population size declines and subsequent genetic diversity losses is not yet characterized.

Given the short generation time of insects, historic specimens with known temporal information (e.g., museum specimens) could be used to evaluate possible declines in genetic diversity and associate these with agricultural shifts and/or land-use change. This would further help clarify whether other processes may be at play in observed patterns of genetic diversity, such as the inflation of nucleotide diversity measures due to non-phylogenetic independence or the interbreeding of previously isolated populations due to habitat loss. Additionally, this study included only those insects that are native to or endemic in North America, meaning the impact of invasive insect species has not been assessed (e.g., Jelbert et al., 2019). Future studies should include non-native species and ideally expand research to other areas of the globe, which are typically underrepresented in ecological research (Van Klink et al., 2020).

Whatever the exact mechanisms of insect population declines, it is undisputed that agricultural intensification and ongoing land-use change are key players in the subsequent losses of genetic diversity and heightened extinction risks. In order to reverse these declines, recent studies have shown that organic farming practices, rewilding techniques, and permaculture alongside increased neighbouring refugia habitats (e.g., prairie strips, forest patches, local nature reserves) can be more effective in regaining biodiversity than popular suggestions like afforestation (Wang et al., 2023). Crossley et al. even observed an increase in genetic diversity in urbanized environments that they hypothesize is associated with more stringent regulations on air and water quality and reduced agrochemicals in areas with high human habitation. They further notice that a geographical concentration of agricultural land post-1950 allowed insect genetic diversity to rebound in other regions. This study therefore provides insight into the ways in which regulation and policy can dramatically impact crucial aquatic ecosystems and offer hope that a shift in current agricultural practices towards a more regenerative system may pave the way to reduce the declines in insect diversity. In the

absence of intervention, these declines are likely to be an ongoing trend of the 21st century, with worrying implications for global food security.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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