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Agriculture sows pests: how crop domestication, host shifts, and agricultural intensification can create insect pests from herbivores

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We argue that agriculture as practiced creates pests. We use three examples (Corn leafhopper, *Dalbulus maidis*; Western corn rootworm, *Diabrotica virgifera virgifera*; Cotton fleahopper, *Pseudatomoscelis seriatus*) to illustrate: firstly, how since its origins, agriculture has proven conducive to transforming selected herbivores into pests, particularly through crop domestication and spread, and agricultural intensification, and; secondly, that the herbivores that became pests were among those hosted by crop wild relatives or associates, and were pre-adapted either as whole species or component subpopulations. Two of our examples, Corn leafhopper and Western corn rootworm, illustrate how following a host shift to a domesticated host, emergent pests 'hopped' onto crops and rode expansion waves to spread far beyond the geographic ranges of their wild hosts. Western corn rootworm exemplifies how an herbivore-tolerant crop was left vulnerable when it was bred for yield and protected with insecticides. Cotton fleahopper illustrates how removing preferred wild host plants from landscapes and replacing them with crops, allows herbivores with flexible host preferences to reach pest-level populations. We conclude by arguing that in the new geological epoch we face, the Anthropocene, we can improve agriculture by looking to our past to identify and avoid missteps of early and recent farmers.

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Introduction

Mythologies of origins typically portray the emergence of agriculture as a divine gift or blessing [1]. Here, we argue that from a pest management perspective, agriculture as practiced is not a blessing because it sows it own pests. We discuss three examples to illustrate how since the emergence of agriculture, agricultural and ecological processes such as crop domestication and spread, host plant shifts, and agricultural intensification, were conducive to transforming selected herbivores into crop pests: Selected herbivores likely were the most-pertinently pre-adapted — as whole species or particular populations — among the herbivores hosted by crop wild relatives or associates. Furthermore, we argue that by looking in the past and around us, while armed with modern ecological, evolutionary and genetic insights and tools, we should be able to predict and pre-empt pests emerging in the contexts of ongoing climate change and ever changing agriculture. While ours is not the first call to look to the past when developing new technologies (e.g. [2–7]), we hope that by reiterating it others will be reminded that while history may not faithfully repeat itself, it typically rhymes [8].

An herbivore in the right place at the right time, and prepared: corn leafhopper

Corn leafhopper (CLH) (*Dalbulus maidis*) is an important maize pest in the Neotropics, and has been associated with maize (*Zea mays mays*) since the crop's domestication [9,10,11•]. Maize was domesticated ca. 9000 years ago from CLH's ancestral host, Balsas teosinte (*Zea mays parviglumis*), and within CLH's native range, the central Pacific lowlands of Mexico [12]. *Dalbulus* consists of grass specialists, mainly on *Zea* and *Tripsacum*, but CLH is atypical among its congeners, for example, it is a strict *Zea* specialist, overwinters in adult rather than egg stage, and is a pest [9,13]. Such particularities suggest that among its congeners, CLH was exceptionally pre-adapted for exploiting maize as it was being transformed to be more productive, but less defended, and as shifting cultivation made it more abundant and widespread, though spatially unpredictable [9,10,11•,14]. Altogether, the available evidence suggests that CLH is a pest of opportunity: When the New World's first-farmers began transforming Balsas teosinte into maize ca. 9000 years ago, CLH among its congeners on *Zea* was likely the species with the standing genetic variation most suited to becoming pestiferous on the new crop, and ubiquitous as maize agriculture spread throughout the Neotropics and became the mainstay of Mesoamerican civilization [9,10,11•,15] (Figure 1).

What does the story of CLH's genesis from herbivore to pest tell us? When most crops were domesticated between ca. 9000 and 4000 years ago, the world's climates

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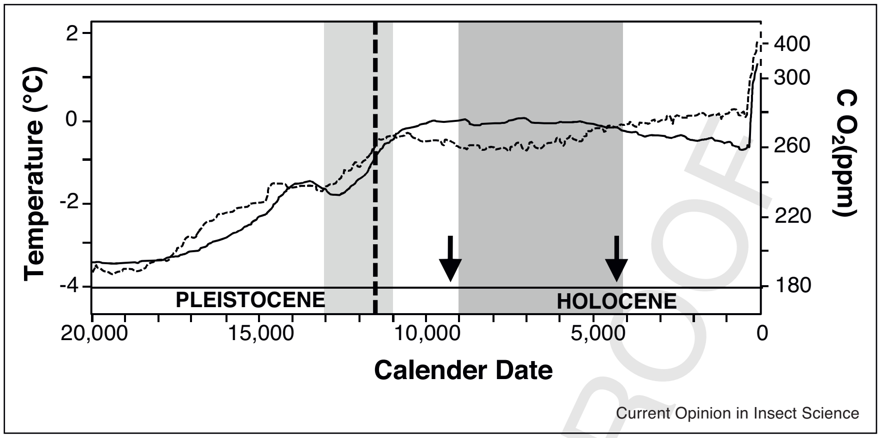
Figure 1



Global trends in temperature (solid line), and carbon dioxide (dashed line) since the end of the Pleistocene (respectively, data shown are global temperature anomalies relative to the early Holocene average over the period 11 500 years before present to 6500 YBP, and atmospheric carbon dioxide composite) (redrawn from [73]). The lightly shaded area (13 000–11 000 YBP) indicates the emergence of farming [78]; the vertical dashed line (11 650 YBP) separates the Pleistocene (to the left of the line) and the Holocene (right) epochs; the down-pointing arrows indicate the beginning of maize domestication and the latest time by which maize landraces were productive enough for the crop to be a staple [12,79], and; the darkly shaded area (9000–4000 YBP) indicates the period during which the rate of domestication of annual crops was greatest [18]. Note change of scale of carbon dioxide composite beginning at 300 ppm.

had largely stabilized after dramatic and fluctuating increases in temperature and CO_2 levels following the Last Glacial Maximum [16–19] (Figure 1). The warmer temperatures and increasing rainfall and CO_2 levels altered plant communities, phenotypes, and interactions with insects [20–22,23••,24••,25,26••,27]. For example, the C_3-dominated forests of the Mesoamerican lowlands ceded ground to C_4-dominated grasslands, and Balsas teosinte became more attractive to hunter-gatherers as they transitioned to farming [21,22,28•]. As host plants were domesticated they offered novel niches to be occupied by the first, pertinently pre-adapted insects to come along. Notably, the extents of climate and CO_2-level changes predicted for the near future are of similar magnitudes to those occurring during the Pleistocene–Holocene transition, notwithstanding isolated, abrupt climate events [16,17,19,29]. Given that the most significant, impending climate changes are decades away we have the benefits of hindsight and forewarning, and must take the opportunity to preempt any pre-adapted, up-and-coming pests of opportunity, such as CLH.

A crop tolerated an herbivore then modern agriculture came along: western corn rootworm

Western corn rootworm (WCR) (*Diabrotica virgifera virgifera*) is a root-feeding coleopteran with a distribution limited to North America — and recently Europe, where it is among the most destructive pests of maize [30]. Like CLH, WCR's genesis as a pest seems to be tied to the spread of maize agriculture: WCR likely adopted maize by shifting from an unknown ancestral host (plausibly the maize wild relative *Zea mays mexicana*) as the crop spread northward from its area of domestication in the Mexican lowlands, and reached the present USA territory <1000 years ago, well after the introduction of maize agriculture [31•]. Over time, it became a pest of maize, especially when it reached the USA Corn Belt in the mid-1900s, when agriculture, especially maize agriculture, were rapidly intensified [30,31•].

Modern USA maize varieties are derived from USA inbred lines, and these descend from USA landraces, which descend from Mexican landraces, themselves descended from Balsas teosinte [32–35]. A de-escalation of plant defenses with crop domestication and breeding is evident across a variety of crops, including maize, and is consistent with ecological theory [14,23••,36,37,38••]. Accordingly, in ongoing studies a trend was predicted in which direct defenses against WCR become weaker with maize domestication and breeding, specifically along a sequence beginning with Balsas teosinte — maize's progenitor, followed by Mexican and USA landraces, and ending with Corn Belt inbred lines, as shown for CLH [14,37,38••]. Additionally, because WCR is a quasi-maize specialist [39,40], tolerance was predicted to increase as direct defenses waned, consistent with ecological theory [41–43,44•]. The results of those studies were remarkably consistent with the predictions, though not across the entire sequence (Figure 2). While indeed maize direct defense de-escalated and tolerance escalated from Balsas teosinte to USA landraces, the trend unexpectedly reverted with Corn Belt inbreds: These showed modest defense and tolerance levels, intermediate

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