Phylogenetic escape from pests reduces pesticides on some crop plants

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Pesticides are a ubiquitous component of conventional crop production but come with considerable economic and ecological costs. We tested the hypothesis that variation in pesticide use among crop species is a function of crop economics and the phylogenetic relationship of a crop to native plants because unrelated crops accrue fewer herbivores and pathogens. Comparative analyses of a dataset of 93 Californian crops showed that more valuable crops and crops with close relatives in the native plant flora received greater pesticide use, explaining roughly half of the variance in pesticide use among crops against pathogens and herbivores. Phylogenetic escape from arthropod and pathogen pests results in lower pesticides, suggesting that the introduced status of some crops can be leveraged to reduce pesticides.

pesticides | phylogenetic ecology | host breadth | herbivore pressure | agricultural ecology

The use of pesticides is among the top means of controlling pests (arthropods, pathogens, and weeds) in crop systems globally (1, 2). Pesticides are considered an essential component of the cost-effective production of food (3). However, the use of pesticides is also considered a substantial ecological threat where pesticide use is linked to the degradation of aquatic systems (4), bird declines (5), the loss of endangered species (6), the loss of pollination services (7), and the evolution of resistant pests (8). To balance the positive aspects of pesticide use with the negatives, it is critical to understand how pesticides are used among crop species. The use of pesticides reflects aspects of a crop's biology, its economic value, and the pest pressure that it experiences (9). We understand the use of pesticides based on crop economics relatively well (10–12); however, there is little information about the use of pesticides among crop plants because of varying pest pressure.

Most crops are grown in regions where they have been introduced by people (13). When plants are moved outside of their native range, they can escape their herbivores and pathogens, resulting in decreased pest pressure (14, 15). Thus, herbivore and pathogen pressure experienced by crop plants is due to two factors: the introduction of pests that feed on a crop and the host expansion of native pests to include the crop (16). The host range of many herbivores and pathogens is defined phylogenetically (i.e., by feeding upon plant species that are related to one another) (17, 18). As such, we hypothesized that crops that lack close relatives in the native flora will be attacked by fewer herbivores and pathogens and experience less pesticide use.

We tested this idea using the 93 major crops grown in California (Fig. 1). All pesticide applications in California against arthropods, pathogens, and weed plants are reported to the state, and data from 2011 to 2015 were compiled into a comprehensive database of pesticide use, reported in applications per hectare per year (*Materials and Methods*). We compiled a list of all arthropod and pathogen species associated with each of the 81 Californian crops where this information was available using the University of California Integrated Pest Management database. We compiled a list of the 4,851 native plant species in California from *The Jepson Manual: Vascular Plants of California* (19). We placed these plant taxa along with all 93 crop species on an ultrametric seed plant phylogeny (20) to estimate phylogenetic dissimilarity between each crop plant and any native Californian plant species (Fig. 1 and *Materials and Methods*). We used this information to conduct phylogenetic comparative analyses of pesticide use and the number of pest species associated with Californian crops. As a negative control, we anticipated that the use of herbicides would not differ based on the phylogenetic relatedness of crops to native plants.

Results

The use of pesticides against arthropods and pathogens decreased with increasing phylogenetic distance from the crop plant to a native plant (Fig. 2 *A* and *B*). As anticipated by economic models, the use of pesticide against arthropods and pathogens increased with increasing per-hectare value of a crop (*SI Appendix*, Table S1). In contrast, the use of herbicides was unrelated to the phylogenetic distance between a crop and the native flora (Fig. 2C) and was instead largely determined by whether a crop was perennial or annual (*SI Appendix*, Table S1). For pesticides against arthropods and pathogens, our models accounted for close to half of the variation in pesticide use among crop species (*SI Appendix*, Table S1), even though pesticide use among crops varied by over six orders of magnitude. As expected, the use of pesticides against arthropods was greater on crops that had more arthropod pests (phylogenetic generalized linear model, t = 2.52, P = 0.01).

Crops with closer relatives in the native Californian flora had a greater number of associated arthropod pest species than crops lacking close relatives in the native flora (Fig. 3 and *SI Appendix*, Table S2). Crops that were planted over larger areas had a marginally greater number of associated arthropod species and a significantly greater number of associated pathogen species (Fig. 3 and *SI Appendix*, Table S2). Differences in the number of native arthropod species accounted for the overall trend toward crops with close relatives in the native flora having greater

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Significance

Pesticides are a ubiquitous component of conventional crop production but come with considerable economic and ecological costs. Phylogenetic escape and crop value determine pesticide use against herbivores and pathogens among diverse crops. Phylogenetic escape from arthropod and pathogen pests results in lower pesticides, suggesting that the introduced status of some crops can be leveraged to reduce pesticides.

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Fig. 1. An ultrametric phylogeny of all Californian seed plants with photographs of representative crops at their phylogenetic positions. Crops shown are (clockwise, from 12:00) oats, wheat, asparagus, onion, mint, tomato, pepper, sunflower, safflower, persimmon, spinach, alfalfa, strawberry, pistachio, cotton, and pomegranate. Photographs are under the Creative Commons CC0 license or the Creative Commons CC3 license via Wikimedia Commons.

numbers of arthropod pests (Fig. 4 and *SI Appendix*, Table S3). The number of native arthropod pest increased with decreasing phylogenetic distance between the crop and a native plant species; however, the number of introduced arthropod species did not vary by phylogenetic distance (Fig. 4 and *SI Appendix*, Table S3). Likewise, more native arthropod pests, but not introduced arthropod pests, were associated with crops that are planted over larger areas (*SI Appendix*, Table S3).

Discussion

Our results suggest that Californian crops that lack phylogenetic relatives in the native flora experience less pest pressure than crops with close relatives. This trend parallels observations of herbivory and pathogen loads in natural systems (21–24). In crops, this suggests that a substantial portion of the damage experienced by crop plants comes from pests that feed on native plants and expand their host range to include the crop plant. Supporting this notion, of the 417 arthropod species listed as injurious pests in California, roughly half (202) are thought to be native, while the remaining species were introduced either with the crop or via other pathways (25). There is substantial evidence that the biota in human-dominated ecosystems, such as farms and cities, is becoming homogenized globally due to a combination of habitat alteration and species introductions (26, 27); however, our analysis suggests that phylogenetically distant crops still escape some potential pests. An increased understanding of crop production, trade routes, and pest species has led to global models of risk to agriculture due to introduced pests (28). Our results suggest that the phylogenetic proximity of crop plants and native flora may improve these estimates.

Attenuation of pest pressure based on phylogenetic distance is likely a universal phenomenon, but it may not be apparent in all regions or in all crops. In our analysis, pesticide use on crops began to decline when the crop was separated from native plant relatives by roughly 30 million y (i.e., during the Oligocene epoch when many major angiosperm genera diversified) (*SI Appendix*, Fig. S1). Thus, pesticide use and pest pressure may not decrease

with increasing phylogenetic distance in regions with low crop diversity or in regions whose crops all have relatively close relatives in the native fauna because that threshold of phylogenetic distance is never reached. In contrast, phylogenetic escape of herbivores may be even more common in places, such as some tropical islands, with low native plant diversity and a high diversity of introduced crops.

We found that phylogenetic distance to any native plant in the Californian floristic region predicted pest numbers and pesticide applications. California is over 400,000 km^2 and includes diverse habitats, some of which are distant from agriculture. A better understanding of the distance over which herbivores colonize crops or other novel hosts may improve our predictions by
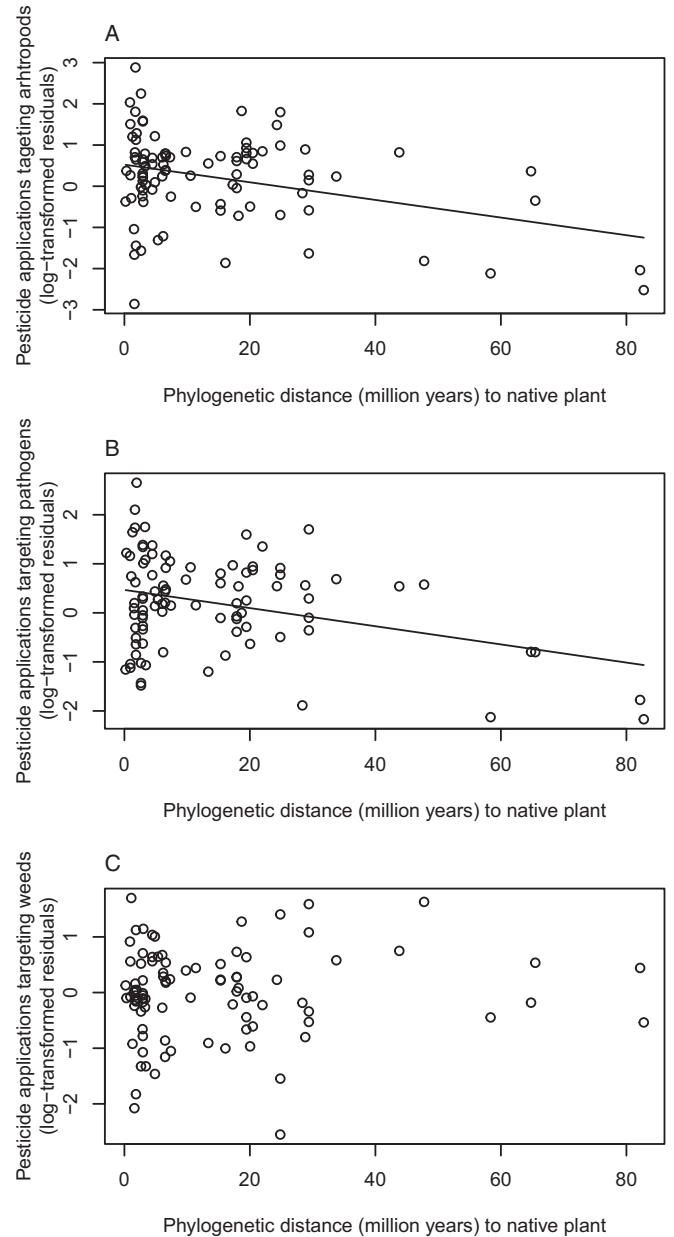

Fig. 2. Pesticide use (residuals) as a function of phylogenetic distance (time to most recent common ancestor) between a crop species and any native Californian plant species. More distantly related crop plants received fewer pesticide applications against arthropods (*A*) and pathogens (*B*) than crop plants with close relatives in the native Californian flora. Relatedness to native plants did not affect herbicide use on crop plants (*C*).
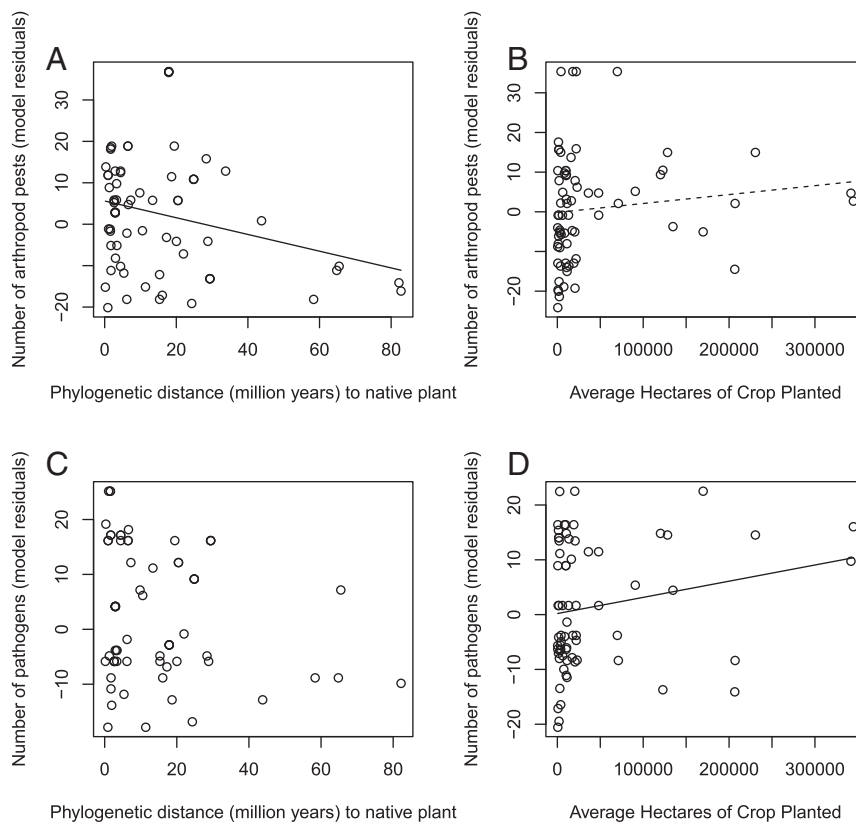
Fig. 3. The number of arthropod (*A* and *B*) and pathogen (*C* and *D*) pest species on Californian crop plants as a function of the crop's phylogenetic distance to any native Californian plant species (*A* and *C*) and the total area of the crop planted (*B* and *D*). More phylogenetically similar crop plants had greater arthropod species richness, and crops planted over a wider area had both more arthropod and more pathogen pest species. The *y* axis is the residuals from a model lacking the key predictor term. Pathogens in *C* and *D* include fungal, bacterial, and nematode pests of crop plants. A dotted regression line indicates a statistically marginal ($0.1 > P > 0.05$) effect.

excluding pests from host plants that are outside of the colonization range.

Phylogenetic predictors of pest pressure and pesticide use are likely related to host expansions of native pests to include a crop. In our analysis, the reduction in arthropod pest richness with increasing phylogenetic distance from a native plant to a crop was driven primarily by a reduction in native pests. We note, however, that phylogenetic predictors may still be useful in predicting host affiliations of introduced pests on introduced crops, although likely in different ways than we show here. Many introduced pests did not historically interact with the crop that they damage, so they have expanded their host range in doing so. The phylogenetic breadth of hosts consumed by that pest (its degree of diet generalism or specialization) and the phylogenetic distance from its ancestral hosts to a crop may help determine its likelihood of establishment (29) and impact (30).

Our study suggests that a biogeographic understanding of pest pressure and pesticide use among crops may be possible based on crop economics, crop traits, and pressure from native and introduced pests. Pesticide use remains a major economic and environmental cost of agriculture. Comparative models of agricultural economics (10), introduced species (31, 32), and injury thresholds (33) can guide actions to optimize the control of pests in crop species and to minimize pesticide use. Phylogenetic relationships have been used to explain major patterns in ecology (34, 35), and there is substantial promise to applying phylogenetic tools to address pressing problems in coping with disease and herbivory (29, 30, 36). We show that phylogeny predicts variation in pests and pesticide use in diverse cropping systems.

Materials and Methods

Pesticide and Pest Species Database. Pesticide and pest databases were compiled after Rosenheim et al. (9) and merged with plant phylogenetic information to form a dataset of pests, pesticide use and phylogenetic information for Californian crops (37). Briefly, for each of the 93 crops grown in California on >600 ha annually, we gathered publicly available statewide data, averaged across 2011 to 2015, on pesticide use (https://calpip.cdpr.ca.gov/main.cfm). Following recommendations from a recent National Academy of Sciences report (38–40), we used the mean number of pesticide applications per hectare per year, rather than kilograms of active ingredient (AI) per hectare, as our metric of pesticide use. Application rates (kilograms of AI per hectare) of different pesticides vary widely, and we were interested in the intensity of control efforts rather than potency of the particular materials applied. We analyzed use of pesticides targeting three classes of pests: 1) arthropods; 2) plant pathogens, including nematodes; and 3) weeds. Pesticide applications were counted as the number of AIs applied. Data on crop value per hectare per year (gross revenues) were obtained from the California Department of Food and Agriculture (https://www.cdfa.ca.gov/statistics/), again averaged across 2011 to 2015. We also collated species lists of crop pests published by the University of California Statewide Integrated Pest Management Program (https://www2.ipm.ucanr.edu/agriculture/) and other University of California Cooperative Extension publications. Pests are generally included in these lists because they have the potential to generate meaningful damage to crops. We found pest lists for 81 of the 93 crops in our pesticide use dataset. Crop-specific pest lists are not available for weed species.

Plant Phylogeny. We compiled a list of all native plant taxa in California from *The Jepson Manual: Vascular Plants of California* (19). We reduced subspecies and varieties to species, and we standardized nomenclature and taxonomic treatment using the Integrated Taxonomic Information System web tool (https://www.itis.gov/). The resulting list had 4,851 plant species native to California. Using this list, we assembled an ultrametric supertree of the
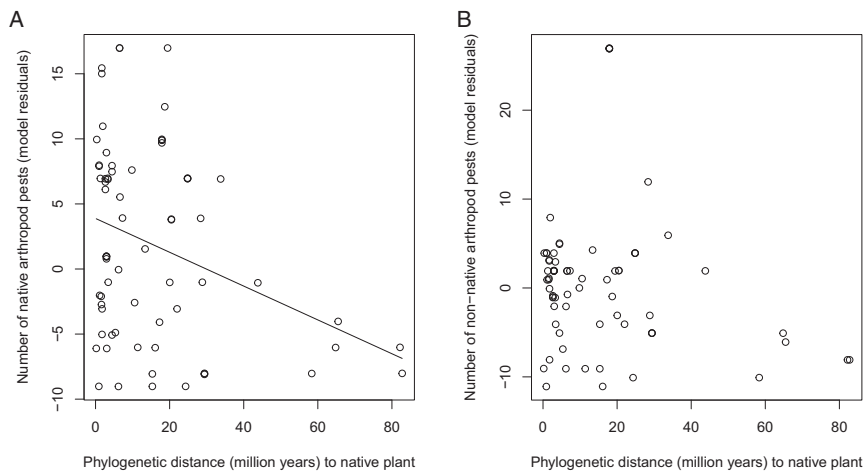
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Fig. 4. The number of (*A*) native and (*B*) nonnative arthropod pest species on Californian crop plants as a function of the crop's phylogenetic distance to any native Californian plant species. The *y* axis is the residuals from a model lacking the key predictor term.

Californian flora. We matched Californian plant species to a recent large ultrametric plant phylogeny (20). Of the 4,851 species, 47% matched tips (species) in the Zanne et al. (20) phylogeny. Of the remaining species, 49% matched a genus on the phylogeny and were placed as a polytomy at the root of the genus. For nonmonophyletic genera, we rooted the added species at the most recent common ancestor of uses of that genus name. The remaining taxa (4%) were placed as polytomies at the root of their respective plant families. Using the same procedure, we also placed each of the 93 crop plant species on the Californian plant phylogeny (Fig. 1). For each crop species, we calculated the minimum phylogenetic distance between crop species and any native Californian plant species. Units of phylogenetic distance (patristic distance/2) are the number of years ago (in millions) since the crop shared a common ancestor with a native Californian plant.

Statistical Analysis. We used phylogenetic comparative methods to test the associations among pesticide use, pest species richness, relatedness of crops to native plants, and aspects of the agronomy of crop plants. For tests of pesticide use, we constructed phylogenetic generalized least squares (PGLS) multiple regression models in which per-hectare pesticide use was a function of the per-hectare value of the crop, phylogenetic distance of the crop to a native plant, the total area of crop planted, and whether the crop is perennial or annual. Pesticide use and crop value were log transformed to meet model assumptions. The PGLS model was allowed to optimize phylogenetic signal (Pagel's lambda), with a starting value of zero. PGLS models were constructed using R (41) packages ape (42) and nlme (43). Pest richness did not conform to a Gaussian distribution, so we modeled pest richness using a phylogenetic generalized linear model using the phyloglm function in the R package phylolm (44) specifying a Poisson generalized estimating equation method (45). Number of pest species was modeled as a function of the phylogenetic distance from a native plant species and the total area of crop planted to account for the potential of a positive species–area relationship (46, 47).

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