DOES A HECTARE OF CROPLAND EQUAL A HECTARE OF WILD HOST PLANT?

In their excellent statement of what was known by 1982 of the forces shaping habitat-level patterns of plant-insect interactions, Strong et al. (1984) concluded that the "recruitment of insects onto British trees must have continued for much longer periods than is apparent either for the newly introduced cacao or sugarcane. . . . This difference is probably a result of the better data from Britain, but we cannot really know." (p. 89.) This conclusion was reached because compared with several crop plants, British wild trees appear to have much larger faunas, per species per unit area for a given time available for colonization.

Here, I would like to suggest that there is a real biological reason why the insect fauna of a newly introduced crop plant should rise rapidly in ecological time but then quickly reach an asymptote and add few or no new species in evolutionary time. In contrast, the fauna of a wild tree introduced to a new area (or arriving as a natural immigrant) should grow more slowly, eventually reach an asymptote at a higher level in ecological time, and continue to add new species over evolutionary time as well. Put most simply, as an island to be colonized, 10^5 km^2 of sugarcane differs fundamentally from 10^5 km^2 of bracken fern, privet, or oak. The first difference is that the sugarcane occurs in large blocks interspersed with blocks of source area from which insect colonists are drawn. In contrast, the wild plant occupies its distributional area as individuals scattered through the original habitats of the source area. If the rate or final level of colonization by phytophages is to be compared with the geographic area occupied by the host plant, the area occupied by a crop plant should be substantially discounted throughout its geographic area as compared with the area occupied by a wild plant. A great deal of a crop plant's acreage is not in the vicinity of any of the source areas. Crop plants, when grown in large-scale commercial plantings, have a built-in distance effect.

Second, there is a negative correlation between the area occupied by a crop plant and the size of the nearby wildland source of phytophagous colonists. As the newly introduced crop is commercially developed, it itself eliminates the source area (unless the source area has already been eliminated by other crops, a situation that exacerbates the process). This sad effect has been particularly prominent with tropical commercial crops over the past hundred years; wildlands have often been cleared for the development of crops on a commercial scale. Additionally, the social changes accompanying the development of a large-scale crop are also debilitating to the carrying capacity of the source area. This is true for species richness as well as for biomass. When a major-crop monoculture

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moves into a previously wildland area, an insect either moves onto it or becomes extinct.

But why is a crop expected to gain its fauna quickly, but a wild plant to do so more gradually? First, a newly introduced crop plant is thrust as a high-density island of food into an ocean of source area. Rarity-of-host effects are minimized. In contrast, the wild plant invades gradually; even in those portions of the habitat that are occupied, the equilibrium density of the invading population may well be too low, too embedded in predator-rich natural habitats, and so forth, to allow an insect to persist or at least to persist until an evolutionary change can occur. Second, over much of the area occupied by the crop plant, the source areas that contribute animals become more distant and smaller as the years pass. In relatively undisturbed areas, such source shrinkage and increasing distance do not occur unless an incoming plant occupies major habitats as thoroughly as does a crop plant. Even when this occurs, the common wild plant's habitat is likely to be interdigitated with other habitats rich in insect species, whereas a crop's vegetation block is likely to be increasingly interspersed with other crop vegetation blocks of low insect-species richness.

To this point, I have avoided the evolutionary aspect of this comparison. However, the long-term evolutionary effects are the same as the short-term ecological effects. When an area is colonized by a crop, the inexorable decline in the size of the insect source area and the increase in distance between the source area and the crop should render the chance of an evolutionary move onto a crop plant ever slimmer with time. In this context, perhaps the amount of crop edge in contact with the source area would be a better variable for species-area contrasts than would be the area occupied by the crop. A wild plant, however, is scattered through its source area; this maximal juxtaposition of potential host and potential herbivore should substantially increase the chance of an evolved move onto it by an insect. Additionally, the peculiar dynamics of crop ecology increase the chance of an evolutionary change in the insect in the early years of crop introduction, before the extinction of the potential herbivores for a new crop. On the one hand, as the proportion of the land used for a crop rises, the proportion of an insect's population that depends on that crop rises (assuming that the crop is a host for at least a portion of the herbivore population). This in turn should minimize the disruption of newly appearing crop-adapted genotypes either by interbreeding with the portion of the population still feeding on wild hosts or by successive colonizations from a wild population. In wild plants, on the other hand, such a phenomenon would occur only if the invading (colonizable) plant species eliminates a substantial fraction of the plants that are hosts for the insects in the source area.

In conclusion, I expect insect species to accumulate more slowly on a newly invading wild plant than on a newly invading crop plant, but through ecological and evolutionary processes to eventually accumulate in greater numbers on the wild plant than on the crop plant. The more the wild host plant is interspersed with the other plants in the area it occupies, the more probable this is. Likewise, the more extensive the crop-plant coverage, the larger the crop-plant area, and the more it accompanies other "modernizing" social changes, the truer this will be.

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