



## Lost Plants

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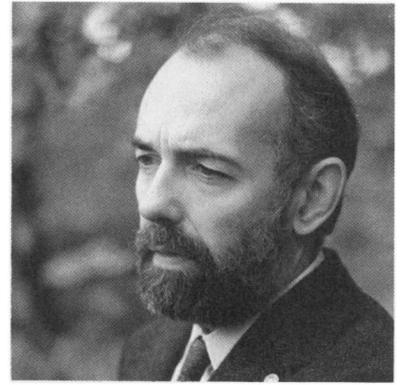
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## Lost plants



Zoologists have long anguished over the recognition and significance of strays, lost migrants, dispersing juveniles, rafting voyagers, etc. Does a migrating bird that is 1000 km from its species' established migration route represent a potential colonist, a victim of strong winds, faulty navigation physiology, or a remnant of a population that has been decimated by recent ecological processes? Are the insects that invade northern croplands each summer, only to be extinguished by winter, a part of a normal natural history being selected for, or is their invasion merely the serendipitous consequence of traits with adaptive significances that are quite unrelated to an invasive natural history? Is a grassland rodent that is encountered in a rainforest treefall part of a breeding population or is it as dead as is a physiologically living rainforest tree seed that is washed up on a Pacific island beach?

Plant ecology is tardy in considering these kinds of questions. In the Neotropical habitats with which I am familiar, I feel that stray plants are a significant fraction of the ecological interactants and are often major contributors to the habitat-level parameters commonly measured by ecologists. In the plant ecology studies currently in fashion, stray plants probably make their biggest impact through contributing what are termed "rare" adult and juvenile plants (including seeds). My focus here is not on the situation whereby a plant is termed "rare" because the habitat where it is common is as yet undiscovered, a situation that applies very frequently to insects that are known only from a few specimens in collections. Nor am I concerned here with plants in populations that depend on a kind of resource or opportunity that occurs at such a low frequency that the plant is always rare.

Consider a habitat structure that is characteristic of many tropical habitat mosaics. In an area of moderate topographic relief, there are a number of distinct habitats. Each has a moderately distinctive flora, yet each also has a number of species in common with some neighboring habitats. When a cluster of such habitats is censused for its plants, it is commonplace to find that the adults of a species of tree are abundant in one habitat, rare in others, and absent from yet others. The

question is, if the habitat where it is abundant is converted to a field, does the remainder of the tree population disappear from the other apparently unaltered forest habitats or is its density significantly lowered in those habitats? The complementary question is, in those natural forest habitats lacking adults of the tree, is it absent in all life stages (including seeds)?

The natural history that I see around me strongly suggests that a substantial number of the tree species (as well as other plant species) that are recorded as rare plants in censuses of the habitat mosaics are in fact strays. When a seed hits the ground, it grows if it can and when its cueing systems say it should. It does not say to itself, "I have fallen in a habitat where my life-long realizable fitness is zero and I therefore commit suicide". An animal may choose to not invest time and material resources in a habitat where it finds itself, and instead move on. A newly arrived plant has no choice but to tough it out, unless the habitat mosaic is so fine that secondary seed dispersal (e.g., erosion) may later move it to a better site. Plant sessility is a large part of what leads to habitats rich in stray plants. Arriving at a site where realizable fitness is zero occurs as a consequence of a parent plant's way of hitting suitable germination sites. By using the "seed shadow" method of locating normal germination sites, the adult plant has a moderate chance of dropping a seed on a microsite or circumstance where the young plant can grow into an apparently normal adult (or superficially similar subadult) even in habitats where this event does not occur often enough to maintain a breeding population. Such physiologically living adults may have zero realized fitness (and therefore be unambiguously not members of the breeding population) because 1) they don't get pollinated, 2) if pollinated, they have their seeds killed by an unsatiated coterie of seed predators, 3) if pollinated, their seeds remain undispersed, or 4) if dispersed, their seed shadow either does not hit the correct habitat or their habitat lacks enough good sites to maintain a breeding population (even though the individual parents grew into apparently healthy adults).

But why does this matter? Why not just label such trees as rare and be done with it?

1) A species of plant that is maintained in the habitat solely by seed flow will only be erratically present in the on-going history of the habitat. If in addition, overall successional changes are occurring on the site, plants may occur that are lost in time as well as in space. For example, when is it reasonable to include senescing or otherwise non-reproducing early successional species of trees in species-richness statements about subsequent later successional seres? In fact, if the species-richness of only breeding populations are tallied in successional seres, many successional seres will be found to be very species-poor even in very species-rich habitats. On the other hand, from the viewpoint of a somewhat generalist seed predator or fruit eater, for example, a successional sere that is poor in plant breeding populations and rich in stray plants might be the very best place to forage. Such an animal may even be getting an evolutionary free ride if all the stray seeds it harvests in the parental successional sere would have died anyway.

2) To a conservationist, the presence of stray plants should be irksome and frustrating. The species richness of a small and newly conserved area may drop dramatically not because of any of the classical island effects but rather because the adjacent habitats – nearby sources of stray plants – are being converted to fields and plantations.

3) The species-packing question of “how does one stack so many species of trees into certain tropical rainforests without the best competitor eliminating the others with similar life forms” is made easier if many of the rare plant species can be viewed as simply strays that are there through chance acquisition of a resource bit, a bit serendipitously and temporarily left unoccupied by a suite of superior competitors. The more sessile a suite of organisms, the more commonplace should be such temporarily unused resource bits. For a tree, an unused bit may be a piece of dirt, a hole in the canopy, a population explosion or invasion of dispersal agents, a once in a lifetime disease epidemic in a competitive dominant, a stray mammoth, or a farmer cutting a tree for a telephone pole.

4) Stray plants should be especially prone to lacking evolutionarily fine-tuned responses to the habitats in which they are growing. Not much time is spent on wondering why a lost eider duck in Florida is carrying a feather load that seems a bit excessive for subtropical climates. The wilt responses of a rainforest vanilla orchid that strays into a tropical deciduous forest via the trade winds may be instructive to the physiological ecologist but are not a product of the orchid's evolutionary past in a deciduous forest.

5) It is commonly the case that habitat occupation is used as an indirect indicator of the physiological traits of a plant species. However, the culling of strays from such a consideration may allow a considerable reduction in the ecophysiological latitude that we often attribute to species of plants. For example, if individuals of a lowland tropical species of oak are found in five distinctive

habitats as acorn-producing adults, but you could know that it maintains a breeding population in only one of those habitats, the task of understanding the evolution of its genome would be considerably simplified. Of like nature, a microsite may be captured by a stray tree and that microsite be adequate to grow what appears to be a normal adult. However, it is simultaneously possible for the area immediately adjacent to that microsite to be so different from that which is usually experienced by the genome that the tree's traits (phenology, growth rates, seed size, leaf chemistry, resistance to herbivores, response to shade, etc.) are quite abnormal for members of the breeding population in the home habitat.

6) Gradients in species density or in species richness across seemingly uniform habitats may not represent undetected gradients in environmental variables of the sort usually considered (moisture, etc.), but rather they may be gradients in proximity to breeding populations that are serendipitously spitting seeds into the other habitats around them. On the other hand, a sharp environmental discontinuity may easily be hidden by seed flow across it, and only very detailed natural history studies of the individual plants will determine to what degree the plants on the inhospitable side of the discontinuity are strays.

7) Plants are a major food for animals, and a given species of animal feeds on a small and select subset of plant species and/or parts in a habitat. Whatever are the within-habitat evolutionary parts of this interaction, it will often be the case that a given species of stray plant will be too unpredictable in time and space to have anything other than serendipitous ecological interactions with the animals that feed on it, even when strays constitute a major part of those animals' diets. While such animal-plant pairs may represent obviously serendipitous matching, at times the matching may also appear to be tightly coevolved; realization that the plants are strays may save anguish over how such a situation could have evolved.

8) The serious study of plants as individuals is finally gaining respectability. At least in tropical habitats, summary statistics on such things as growth rates, survivorship, fruit set, etc. will evermore be derived from tables of long-term histories of individually numbered and followed plants. If one could cull the strays from these tables, or at least put them in separate tables, I suspect that much of the variance would be removed. Likewise, even within the breeding population, it is evident that such sorting of individuals with respect to their realized fitness would be of great value with respect to understanding the congruence between the realized fitness and fundamental fitness of what appear to be healthy adult plants.

9) As electrophoretic and other methods of genetic analysis give us plant parentages in complex forests, it is clear that discrimination between strays and breeding populations is essential when characterizing genetic structures of populations. In analyzing the genetics of

California bird populations, one does not want to indiscriminantly include the genomes of strays from the central United States migratory flyway 1000's of kilometers to the east. The same applies to adult stray plants that are the products of regular or episodic overlap of seed shadows originating in somewhat different habitats, each of which contains a distinctive genome of a widespread species. Yes, such invading plants may inter-

breed with the residents, but the interpretation of the invaders' genomes and those of the hybrid offspring should be different from that of the resident population.

How does one recognize stray plants? The same way one recognizes a stray dog.

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