On Ecological Fitting
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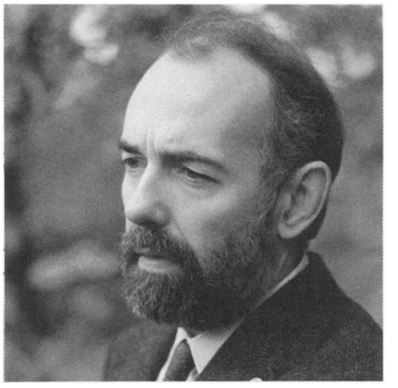

Dan Janzen's thoughts from the tropics 1

On ecological fitting

I've grown up on a diet of Darwin, Wallace and their cultural offspring. But I'm faced with the reality of the biology of 100 km^2 of lowland dry forest (Santa Rosa National Park) in northwestern Costa Rica. Some of my background does not prepare me for this: almost all the ecology I see around me could quite easily come to be with virtually no evolution having occurred at Santa Rosa.

Santa Rosa is a very ordinary place. The fine-scale mosaic of habitats ranges from 30-m-tall nearly evergreen forest to 2-m-tall deciduous thorn scrub, with a variety of anthropogenic successional seres. There is a 0–350 m elevation range, 900–2300 mm annual precipitation, and two dry seasons, one of which is about 6 months long and usually rain-free. Santa Rosa's habitats are quite literally crawling with complex biotic interactions. The participants number at least 650 species of plants, 3100 species of Lepidoptera, 200-plus species of seed-predator beetles, 58 species of mammals, 250-plus species of birds, and many more. It's decidedly tropical.

The problem is that at least 98 percent of these species have geographic ranges covering tens of degrees of latitude. While the majority are common and widespread in the dry Neotropics, another majority ranges widely over low elevation rainforest habitats as well. Over their wide ranges, these species interact in many complicated ways with many other species that do not occur at Santa Rosa. However, these wide-ranging species are made up of similar, if not apparently identical, individuals in quite different parts of their ranges.

The implications of these observations are difficult to reconcile with the commonplace view of a species as evolutionarily labile. This difficulty leads me to wonder if a profitable excursion in evolutionary ecology might be to explicitly introduce some heterogeneity into the ability of natural selection to mold genomes. As I write that, I suddenly realize that I have blundered through the front door of the turmoil over punctuated equilibria. We don't have to dig at the fossil record; punctuated equilibria are right here in front of us, represented by most of the species that you and I have anything to do with.

I am here concerned with any region that is primarily occupied by species with the following cyclical pattern to their histories. Furthermore, these species are in the evolutionarily quiescent stage in the cycle during their occupancy of the region. Initially, a species is a small population occupying a small area. Such a restricted occupation occurs through foundling establishment, habitat fragmentation, habitat shrinkage, etc. This population evolutionarily passes through a succession of genotypes. This change occurs because the habitat occupied changes and because the small population is being evolutionarily fine-tuned by selection to the particular traits of the habitat it occupies. Then, the population abruptly expands out of its local habitat in the duration of a few generations. The expansion occurs because the evolving population happens upon some genotype that is serendipitously robust with respect to the challenges of living throughout some large geographic area. It may also occur because some geographic barrier has been relaxed (or bypassed), or because major abiotic changes make a small habitat into a widespread one. The species is now widespread. By virtue of being huge, widespread, on an adaptive peak, and subject to a multitude of selective pressures that are fine-scale heterogeneous and contradictory, the species now becomes evolutionarily static. It is only likely to evolutionarily change when a new genotype appears that raises fitness throughout much of the species' range. It then continues to be a widespread species until some sort of major perturbation occurs throughout its range, whereupon it is extinguished or reduced to some small population that is again evolutionarily labile. Likewise, during its tenure as a widespread species, isolates occur from time to time, and a very minute fraction of these start the cycle again.

It appears to me that Santa Rosa is almost entirely occupied by species with such cyclical histories and that they are occupying the site during the widespread phase of their histories. Furthermore, it appears to me that most continental habitats are occupied as is Santa Rosa.

When such a species breaks out of its local status somewhere and arrives at a site such as Santa Rosa, what happens? Think in terms of Africanized honey bees, cattle egrets, feral cattle and guanacaste trees (or gypsy moths, ring-necked pheasants, feral house cats and kudzu). It will come to occupy some, but not all the habitats at the site. If it is a plant, its flowers will be pollinated to various degrees and qualities in different habitats. Likewise, its seeds will be dispersed to various degrees and into various patterns of seed shadows, which will in turn impinge upon a wide variety of habitats. Only some of these habitats will contain members of the plant population. Its foliage will be fed on to various degrees in different habitats and its fitness will be variously reduced in these different habitats as a consequence. Of the habitats it occupies, in some it will be very common and breed, in some it will be less common and breed, and in others it will be present only as strays (be they adults or juveniles). These various levels of habitat occupation will also be generated by the more traditionally considered variations in physical environment and impact of other plants. If an animal, all the above kinds of interactions will occur, and with the same consequences. In short, our newcomer will be patchily distributed, variably abundant, and have different interactions with different organisms in the various habitats of the Park.

No evolutionary change was necessary or likely for our invading species to incorporate Santa Rosa into its range, and to develop the heterogeneous microdistribution and microexpression of its fitness that it now has. Furthermore, there is no reason to expect that the established residents did anything other than ecologically readjust to this act of ecological fitting. All imaginable levels of readjustment may occur, from going extinct to no response. Almost all the complex interactions now at Santa Rosa may be nothing more than the consequences of a long succession of ecological fittings of one wide-ranging species after another.

While seemingly innocuous, trite and obvious, I have constructed an argument that roughly suggests that a major part of the earth's surface may be occupied largely by organisms that are rich in ecological interactions and have virtually no detailed evolutionary history with one another. In such a view, questions such as "What are the selective pressures maintaining such and such a set of traits of an organism" would need to be severely augmented by "What might have been the selective pressures that invented such a set of traits", "What blocks their decay", and "What are the ecological processes that lead to such and such a kind of ecological fit"?

Santa Rosa is occupied by a medium-sized saturniid moth with hind wings bearing brightly-colored large eye-like spots (*Automeris io*). This moth ranges from Canada to Costa Rica and has virtually identical adults over this range. Which is the more reasonable explanation of these false eye spots?

1) Through a range of 40 degrees of latitude, in habitats ranging from Illinois roadside ditches to a Costa Rican forest that contains 200-plus species of visually-orienting vertebrate potential predators, the selective pressures are sufficiently similar to maintain this single phenotype.

2) The phenotype is evolutionarily frozen and the moth occurs wherever its realized fitness is great enough for persistence. In some habitats, the eye spots are highly functional in deterring predators, but the moth is absent because its larval host plants are absent. In some habitats, the eye spots and the behaviour of displaying them simply lead to increased predation by (too) smart predators, but the moth remains a common member of the fauna because there are massive amounts of parasitoid-free host plants. In some habitats, the eye spots are highly funtional and that is why the moth is present. Finally, in some habitats the eye spots are simply irrelevant because there are no significant visually-orienting predators, but the moth is only occasionally present because only in some years is there enough rain for the host plant's seeds to germinate. So, when a mutant appears that modifies the eye spot so as to raise the moth's fitness in but one of the many habitats it occupies, it seems reasonable that it does not spread throughout the moth's range. However, it also seems likely that such a mutant might persist in some small isolate of *Automeris io* occupying only one habitat.

If this approach is not all nonsense, then in determining the processes that lead to structure in habitats we should concern ourselves with the ecological outcomes of successive introductions into a habitat, as well as with the evolutionary adjustments among species. There is, then, a strong esoteric rationale for the study of habitats rich in introduced species. On the one hand, it is tempting to critically note that easily 99 percent of the papers in esoteric ecological journals today deal with "native" animals and plants. On the other hand, easily the same 99 percent applies to widespread organisms in habitats so modified by recent humans that the organisms might as well have been introduced. The rationale that I present here also gives very special meaning to the study of the natural history of small, local or otherwise evolutionarily labile populations. What gives a species its traits, what makes it "successful", may have little or nothing to do with its evolutionary history while it is a widespread species.

There are two quite different ways that a habitat may come to have its traits. For example, does an extra-tropical habitat accumulate a set of caterpillar species that feed primarily in the spring and autumn because 1) the species that are there have been selected to feed at that time by the traits of the plants and the carnivores at those times of year, or 2) as species after species arrived at that habitat over the past, those that persisted were those that had the right stuff for those times of year, while those that failed were species that had mid-summer caterpillars and life is miserable for mid-summer caterpillars? Are some of the plant species at Santa Rosa quite free of herbivory because here, as well as throughout the rest of their ranges, they have evolutionarily repulsed each species of herbivore that found the plant? Or, is it that such a plant evolved some particularily effective deterrent when it was a local population somewhere and then spread with this trait throughout its contemporary wide range? Is an ostentatious toxic butterfly the color here at Santa Rosa that is best for advertisement to the predators here? Or is it simply that particular bright color because its phenotype worked well somewhere, and works well enough for persistence at Santa Rosa despite the fact that some mutant might well have a higher fitness at Santa Rosa?

I predict that there are some large and fruitful surprises to come out of questions such as

1) What properties should the array of species in a habitat display if all arrived sequentially with their personal traits evolutionarily frozen, and then simply made it to some degree?

2) How does one distinguish between multispecies mutualisms that evolved vis a vis the mutualism, and those that are the consequence of ecological fitting (e.g., introduce agoutis to Africa, and then determine how the resultant mutualisms differ from those in the homelands of Neotropical agoutis)?

3) What were the intensive interactions in small populations that produced the salient traits of the large number of widespread species that we study today?

4) What will be the consequences of arbitrarily chopping out a small block of terrain occupied almost entirely by widespread species and overnight converting them to local species (the biological history of almost all National Parks and Reserves around the world)?

5) Can we consider the chemical defense traits of plants as simply one more trait that leads to persistence of the plant in a herbivore-rich habitat, rather than as a trait selectively maintained by all those herbivores that do not feed on the plant (i.e., when leaf-cutting ants are introduced to Africa, the resultant food choices they display will certainly not be coevolved)?

6) What are the decay rates of traits in nature once a species becomes widespread, and what internal as well as external processes determine the heterogeneity of those rates (i.e., to what degree does the phenotype prevent decay of the genotype)?

7) What are the properties of serendipitous multipurpose traits (e.g., what ecological processes could convert a non-migratory species into a migratory species, rather than asking how did migratory traits evolve)?

8) How do all those species get packed into tropical habitats without eating each other up or squashing each other (as opposed to "how did all those species evolve in the tropics")?

9) What sorts of habitats should be particularily important in spinning off lots of widespread species, and what sorts of habitats should primarily accumulate and maintain local species?

10) What are the detailed events that actually stop an invading widespread species?

The complex interactions enacted by introduced species of animals and plants all over the tropics make it quite clear that a species does not have to evolve in a habitat in order to participate in the interactions in that habitat. Widespread species are not adapted to their habitats, they just are. In fact, it can even be argued that most members of most widespread species are quite maladapted to their habitats. As anyone knows who has suffered a setback in life, you don't have to be well-adapted to survive. You just have to survive. We are all asymmetrical pegs in square holes.

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