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THE RISE AND FALL OF PLANT SPECIES: A POPULATION BIOLOGIST'S PERSPECTIVE[1]

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These are exciting times for plant evolutionary biology. Molecular data, new analytical techniques, and thoughtful experiments and syntheses are providing insights into many classic issues, including phylogeny and character-state evolution at every taxonomic level (e.g., Barrier et al., 1999; Panero et al., 1999; Soltis et al., 2000a, b; Pryer et al., 2001; Sytsma and Hahn, 2001), patterns of adaptive radiation (Givnish and Sytsma, 1997a; Les, Cleland, and Waycott, 1997; Baum, Small, and Wendel, 1998), the history of geographic differentiation within and among species (Wagner and Funk, 1995; Wen, 1999; Abbott et al., 2000; Givnish et al., 2000; Schaal and Olsen, 2000; Wright et al., 2000), gene flow and spatial scales of genetic differentiation within and among populations (Wolf and Soltis, 1992; Hamrick, Murawski, and Nason, 1993; Nason, Herre, and Hamrick, 1998; Cain, Milligan, and Strand, 2000), the impacts of hybridization and polyploidy on speciation, adaptation, gene expression, and chromosomal evolution (Arnold, 1997; Rieseberg, 1997; Burke, Voss, and Arnold, 1998; Cook et al., 1998; Husband and Schemske, 1998; Brubaker, Patterson, and Wendel, 1999; Cronn, Small, and Wendel, 1999; Rieseberg, Baird, and Gardner, 2000; Soltis and Soltis, 2000), the concordance of genomic architecture among closely related taxa (Moore et al., 1995; Wendel, 2000), the genetic bases for reproductive isolation via specialization on different pollinators (Bradshaw et al., 1998; Schemske and Bradshaw, 1999), and the genetic evolution of certain key aspects of floral development (Meyerowitz, 1994; Doebley and Wang, 1997; Albert et al., 1998; Baum, 1998; Bowman et al., 1999).

Given these remarkable developments, and the three decades that have elapsed since the last comprehensive—and magisterial—treatments of plant speciation and evolution by Grant (1971) and Stebbins (1971, 1974), it was with the greatest interest that I awaited Don Levin's new book *The Origin, Expansion, and Demise of Plant Species.* Levin was a hero of my youth, who had made his name in plant population biology, but also added substantially to our understanding of speciation through his research on the genus *Phlox* (Polemoniaceae). His contributions included early studies of plant demography, genetic differentiation among populations, divergence in pollination biology among closely related species, selection for reproductive isolation, and constraints on species ranges.

Levin's intriguing premise is that we can best understand plant evolution if we view plant species as having a life cycle, from birth to geographic expansion, genetic differentiation and diversification, increasing disunity, and ultimately death through extinction. Levin argues that the evolutionary trajectory taken by each species should depend on the nature and organization of its genetic variation, its dispersal ability, and ecological interactions with competitors, predators, and mutualists, and the habitats it encounters, but that, nevertheless, different species should show several similarities if they occupy a similar life-cycle stage. After birth, species should rapidly acquire genetic variation, expand in range, and undergo genetic differentiation; aging should be manifested by the contraction and/or fragmentation of geographic range, loss of genetic variation, and increased likelihood of extinction. The evolutionary trajectory taken by a species should depend on its own genetic and ecological attributes, as well as its interactions with a changing physical and biological environment. Levin thus asserts that ecological issues must take equal place with the genetic ones traditionally considered if we are to understand the evolution of species.

This proposal makes good sense: ecology helps determine the nature of the initial divergence of species from their progenitors, sets the stage for subsequent adaptive evolution, imposes constraints on gene flow and thus speciation rates, subsequent range expansion, and geographic differentiation, and saddles species with an ever-increasing burden of competitors, herbivores, pests, and developmental and genetic constraints. The nature of genetic variation, in turn, helps determine a species' response to these ecological pressures.

Levin develops these themes through nine chapters, devoted to (1) the historical framework just given and a brief review of species concepts, (2) the ecological bases of speciation, (3) the genetic bases of speciation, (4) the geographic scale of speciation, including a critique of traditional models of geographic speciation, (5) range expansion and species limits, (6) genetic differentiation and the loss of cohesion through the formation of ecological and chromosomal races, (7) species decline and extinction, (8) the ecological and genetic mechanisms by which existing species may interfere with the rise and further evolution of incipient species, and (9) species' longevities and how they may vary with ecological conditions. The book is a review and synthesis of previously published work, with almost no new data, concepts, or overarching theories developed for the book itself. Chapters begin with a brief statement of Levin's views of the ecological and/or genetic issues involved in a particular topic, followed by a lengthy enumeration of empirical findings supporting this perspective, and concluding with a short overview.

While exciting in prospect, Levin's magnum opus is, alas, a serious disappointment in its realization. We immediately get into deep water in Chapter 1 with a baffling discussion of species concepts, a fundamental issue for any book with the ambition to reshape our views on plant speciation. Even though this subject has been treated incisively by Mayr, Stebbins, Grant, and many other luminaries—and even though Levin cites these authors as well as recent symposia (e.g., Howard and Berlocher, 1998) that vividly capture the vigor and rigor of current debate—Levin's treatment is the least

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thoughtful, least helpful discussion of species concepts that this reviewer has encountered in the modern literature. After disposing casually with the biological species concept, taxonomic species concept, and many others, Levin advances what he calls the ecogenetic species concept on pp. 10–11:

> The limitations of any species concept notwithstanding, I am obliged to employ one, since this book deals with the origin and fate of species. I propose that each species has a unique way of living in and relating to the environment and has a unique genetic system—that is, that which governs the intercrossability and interfertility of individuals and populations. I will refer to this as the Ecogenetic Species Concept.

This Delphic definition—even if it were rephrased so as to be grammatical, highlight the centrality of mating barriers, and not involve infinite regress—hardly seems operational or biologically reasonable. Which species, as recognized under current concepts, would not have a unique ecology and a unique genetic system? Wouldn't the slightest difference in physiology and genotype distributions between populations qualify each as ecogenetic species, even if the difference were caused by only a single individual? What about many taxa in sedentary groups, like the bromeliad genus *Navia* from the Venezuelan tepuis (Givnish, 1997), which have repeatedly speciated in allopatry in the near-absence of gene flow, but have diverged rather little, if at all, from each other ecologically? Should species that diverge little ecologically and are now allopatric, but once overlapped in range, be distinguished from similar taxa that have always been allopatric? Levin's subsequent statement that "good ecogenetic species may hybridize" further confuses the issue: What is a "bad" ecogenetic species? Are ecogenetic species a subset of those recognized under the biological species concept, based on partial or complete reproductive isolation, or do they exist on some other plane, defined in part by their degree of ecological divergence?

Most students of speciation have agreed that reproductive isolation among pools of interfertile populations is the key feature defining and separating species (e.g., Mayr, 1942; Bradshaw et al., 1998). Such reproductive isolation can, in principle, occur with or without ecological isolation of the noncrossing entities. Indeed, selection for ecological isolation may be most effective only after reproductive isolation is achieved and would be biologically relevant only when taxa overlap in their actual or potential ranges. Why should we recognize as species only those that are ecologically isolated and have overlapping or abutting ranges, in addition to being reproductively isolated? Including in the species definition the Lackian hypothesis that selection should favor the evolution of ecological isolation among closely related species precludes testing that hypothesis and so should be avoided, if only on philosophical grounds. Given all of the above concerns, and that Levin himself states that ecogenetic and taxonomic species will often be equivalent, it seems unlikely that botanists will adopt Levin's definition in droves. More importantly, the use of a shaky species definition undermines the book's very foundation.

Given the supposed importance of ecological divergence, it is remarkable that Levin devotes less than three pages of Chapter 2 to adaptive radiation itself, even though it is perhaps the most important process bridging ecology and evolution. Levin displays little or no cognizance of several key papers that have recently appeared on adaptive radiation in plants, including several in *Molecular Evolution and Adaptive Radiation* (Givnish and Sytsma, 1997a). This is a major shortcoming. As detailed by Givnish (1997), there are many crucial, interrelated issues involving phylogeny, ecology, adaptation, biogeography, genetics, and development imminent in any adaptive radiation, and few of these are even broached by Levin.

For example, in very few supposed cases of adaptive radiation in plants do we have compelling data showing that the divergence among species is actually adaptive (i.e., increases fitness). This salient fact is not mentioned, although there are now three research teams pursuing this issue. Essential to such efforts are (1) a phylogeny to allow independent comparisons among close relatives and (2) measurements of differences in fitness or growth in common gardens, greenhouses, and/or field sites under different conditions. Common-plot studies are key because different species in a radiation often grow in different habitats, so some of the "species" differences may simply reflect acclimation to different conditions. Ultimately, knowledge of the genetic control of phenotypic variation is also needed for an in-depth understanding of species responses to divergent selection, as so ably exemplified by the research of Bradshaw et al. (1998) and Schemske and Bradshaw (1999) on selection for floral traits associated with bee vs. hummingbird pollination in *Mimulus.* These studies involved measurements of fitness under field conditions, characterization of the pattern of phenotypic inheritance, and inferences regarding phylogeny based on molecular data, and illustrate how future studies might allow us to investigate adaptive radiation via a fusion of molecular genetics, molecular systematics, and ecological experiments furthering the spirit of Clausen, Keck, and Hiesey. One crucial aspect of this work that Levin fails to note (even though it is central to the genetic bases for speciation discussed in Chapter 3) is that the key traits favoring pollination by bees vs. hummingbirds in *Mimulus lewisii* and *M. cardinalis* are controlled by just a few loci. This genetic architecture would allow selection for pollinator specialization—and hence, for reproductive isolation and speciation—to proceed very rapidly.

A central question involving adaptive radiation is whether ecologically similar species in a lineage are closely related, convergent, or both. Most classic studies of adaptive radiation are flawed because the very characters under study (e.g., beak size and shape) were also used to infer relationships among the species in question, raising the possibility of tracing traits down evolutionary branches determined, at least in part, by themselves. To avoid the possibility of such circular reasoning—and phylogenetic inferences led astray by convergence (or the concerted convergence of several different traits in species invading similar habitats [Givnish and Sytsma, 1997b; Givnish and Paterson, 2000]), many researchers now infer phylogeny from molecular data and then deduce patterns of adaptive radiation by overlaying phenotypic characters on the independently derived molecular phylogeny. With few exceptions, Levin never makes clear why he says particular species are closely or distantly related, and the possibility of circular reasoning, involving inferences based on morphological similarities, not even formally analyzed, raises doubts about much of what was said regarding evolutionary trends.

More generally, the book's most glaring flaw is its failure to incorporate a phylogenetic perspective. Modern readers may be surprised to find but a single cladogram in a book largely devoted to speciation. This alone prevents many exciting (indeed, revolutionary) contributions, based on plant molecular systematics and phylogenetic analysis and listed at the outset of this review, from being presented effectively. To be sure, Levin's treatment of microevolutionary issues (e.g., genetic structure, selection, gene flow, the mechanics of reproductive isolation) is more solid. But his avoidance of most macroevolutionary issues, and the data now available to address them conclusively, makes for a much less compelling treatment. Most importantly, it denies Levin the critical data he needs to assign species to different stages in the putative species life-cycle (see further comments on this below).

One area where the lack of a phylogenetic perspective and critical accompanying data is keenly felt is in the treatment of geographic speciation in Chapter 4. Partly this is a matter of bad timing: Levin was completing his book just as phylogeographic studies of evolution, historical patterns of dispersal, and genetic differentiation within species were beginning to hit their stride in plant groups, involving research on movement from glacial refugia in western Europe (reviewed by Abbott et al., 2000) and differentiation in cassava in tropical Brazil (Schaal and Olsen, 2000). It has proven much more difficult to obtain the kinds of hypervariable markers required for phylogeographic studies in plants than in animals, where mitochondrial DNA sequences and restriction sites have proven highly illuminating. Research by several zoologists has shown, for example, that sister species in several tropical faunas appear to have diverged long before their isolation in Pleistocene refugia, and that areas of greater habitat heterogeneity and/or climatic or geological upheaval support more taxa of recent origin (Moritz et al., 2000). Now that useful markers for phylogeographic studies have been developed for plants, it will be interesting to see whether similar patterns emerge for tropical and temperate floras. Once the relative ages and distributions of species, subspecies, and groups of populations are identified, it should also be possible to conduct rigorous tests of ideas regarding the evolutionary trajectory of genetic variation and geographic differentiation following speciation. An important unresolved question is whether the markers that ultimately prove useful in plants will be coalescent (e.g., cpDNA sequence variation) or highly noncoalescent, with substantial polymorphism within and among populations (e.g., AFLP markers). Phylogeographic studies will prove much more difficult if noncoalescent markers are required.

Levin is deeply skeptical of phylogenetic reconstructions of the speciation process and the geographical scale at which it operates. This is partly because he disagrees with the cladistic view that ancestral species necessarily lose their identity when they ''split'' into daughter taxa. Levin believes, quite rightly, that geographic speciation in small satellite populations can occur with little or no change in contemporaneous ''ancestral'' populations. But this is a red herring; cladistic analysis can recover this kind of process, with short or null branches along the ancestral branch ''sister'' to those of the peripheral isolates. Phylogeographic studies are really essential to test the hypotheses of genetic differentiation that Levin advances based on microevolutionary principles.

Levin criticizes what he views as the traditional model for geographic speciation because ''there is no effective mechanism'' to bring about collective genetic change across the range of a species or ecological race. He argues that single populations cannot themselves be the unit of speciation, because they are too vulnerable to extinction. Levin concludes that metapopulations—aggregations that are linked by the foundation of new populations via colonization and local extinction of existing populations—must lie at the base of the speciation process, involving small enough aggregates to allow rapid genetic change via selection and population bottlenecks, but a large enough number of populations to prevent untimely extinction of the differentiating genetic system, interacting with each other weakly enough so that gene flow doesn't swamp adaptation to local conditions. Judging from the fact that exactly two journal articles on plant speciation have cited this mechanism since Levin published it in 1995, speciation via metapopulations looks like a hard sell. I also feel that Levin misrepresents the views of previous authors regarding geographic speciation in advancing ''his'' model and that he glosses over several important questions regarding his own metapopulational model. Ernst Mayr may be surprised if he were to read Levin's characterization of traditional geographic speciation! No one did more than Mayr (1963, 1970) to champion the role in geographic speciation of peripheral isolates, that is, small populations or groups of populations beyond the continuous range of a species, frequently founded via long-distance dispersal or the rise of new habitat barriers. Mayr discussed how genetic change could sweep through individual isolates much more rapidly than through the continuous range of a species. In addition, beyond the factors discussed by Levin, Mayr argued that peripheral isolates would foster intense inbreeding and the consequent loss of genetic background and breakdown of what he envisioned as ''coadapted genotypes,'' facilitating rapid phenotypic evolution and speciation. At times, Levin appears loath to acknowledge others as the originators of ideas he feels are his own. This happens repeatedly with regard to geographic speciation (Mayr), chromosomal evolution (Stebbins), character displacement (Mayr), purging of inbreeding depression (Lloyd, Solbrig), and selection for reproductive isolation among populations whose hybrids exhibit reduced fitness (V. Grant and several others).

These issues aside, there are several questions regarding speciation via metapopulations. What is the desired balance of reduced likelihood of extinction with the retardant effects of homogenizing gene flow, and how would this balance shift with the size, connectance, and dynamic turnover of individual metapopulations? Is speciation more likely to occur in metapopulations than in independent populations having the same number as those composing the metapopulations? If so, why? If speciation does occur within a metapopulation, how could we show that the crucial genetic changes did not take place in a single component population first or critically depended on mechanisms that operate only at the metapopulation level? Why wouldn't the rise of reproductive isolation within a single population lead to speciation, whether or not that population were part of an integrated metapopulation at that time? I am highly sympathetic to the ecological importance of metapopulations and to the need for greatly expanded research on metapopulational genetics, but speciation via metapopulations does not seem likely to be an important new insight.

The near absence of a discussion of mechanisms of sympatric speciation was notable; even polyploidy, mentioned at several points in the text, has no treatment in Chapter 4. The remarkable case of *Stephanomeria malheurensis* (Gottlieb, 1973) is barely mentioned. This species was endemic to a single volcanic outcrop in Oregon, where it grew with what appeared to be the parental species, from which it appeared to have been recently derived in sympatry via Robertsonian chromosomal translocations and inbreeding. Levin later insists

(Chapter 6) that the only compelling instance of reproductive character displacement in plants—presumably involving sympatric reinforcement, if not speciation itself—is one he and his colleagues studied in *Phlox drummondii*, which shifts its flower color where it overlaps with *P. cuspidata.* This is indeed a very important case, but other instances that vividly illustrate this principle are overlooked. Grant (1966) showed, for example, that sympatric or peripatric species of *Gilia* in North America or South America were much more likely to exhibit mating barriers than allopatric pairs of species occurring on different continents. Hapeman and Inouye (1997) found that closely related species of the temperate orchidoid genus *Platanthera* that are sympatric or peripatric are quite likely to differ in placing their pollinia on the proboscis vs. eyes of pollinators. Soliva and Widmer (1999) recently showed that early- and late-flowering races of *Gymnadenia conopsea,* which occur sympatrically, are reproductively isolated; their molecular data are consistent with multiple origins of differences in flowering time.

While Levin discusses the key process of gene flow in detail, his treatment slights the importance of seed movement. True, pollen often moves further than seeds, but seed movement is required for invasion of new territory, and the most extensive gene flow occurring in species may involve the expansion and contraction of their ranges during climatic oscillations. As the recent work by Cain, Damman, and Muir, (1998) makes clear, microevolutionary data on contemporary gene flow in wild ginger (*Asarum canadense*) is consistent only with movement of a few tens of kilometers from its Pleistocene refugia, compared with its actual movement of roughly 1000 km. Clearly, occasional long-distance seed dispersal has played a major role in the range expansion of many species; such long-distance gene flow may have also played a key role in affecting genetic divergence at different spatial scales and incipient speciation (e.g., see Mitton et al., 2000). In one species-rich group after another studied by my colleagues, students, and myself—*Banksia*, *Calochortus*, *Cyanea*, *Navia*—extensive speciation and narrow endemism are associated with poor powers of seed dispersal, involving unwinged or heavy seeds that are passively dispersed or fleshy fruits in rainforest understories dispersed by forest-interior birds, which are themselves notoriously sedentary.

Levin's treatment of the ecological factors limiting the spread of species and constraining their geographic distributions (Chapter 5) is provocative and largely successful, drawing heavily on recent work by D. and P. Soltis on the present-day origin and spread of polyploid weeds (e.g., *Tragopogon*). He repeats the familiar argument that gene flow from the interior of a species' range can swamp peripheral populations and act as the principal factor preventing increased adaptation to local conditions and advancement of a species' distributional limit. But the effects of gene flow on local adaptation are likely to be nonmonotonic, with very low levels unlikely to swamp populations and yet providing the crucial influx of new mutations on which local selection must operate. It would be interesting to know if Levin's claim is true that population turnover (extinction and founding events) is more frequent near a species' range limit. And, if gene flow uniformly retards local adaptation and expansion of range limits, why is it that many wind-pollinated tree species—presumably with very high amounts of long-distance gene flow—often have the widest ranges of any ecological plant group in North America? How important instead are natural enemies (disease, closely related competitors, predators) and the coevolutionary pressures they create in limiting plant species distributions over ecological and evolutionary timescales?

I would suggest that another, as yet unexplored factor limiting species distributions may involve the spatial autocorrelation of environmental conditions. In any given area, there should be selection for individuals to depend on the most reliable, informative environmental signals (e.g., daylength) to trigger developmental plasticity adapted to the underlying ecological conditions (e.g., temperature, rainfall) correlated with those signals. Gene flow and the spatial autocorrelation of environmental conditions should ensure the adaptive value and shared use of the same signals throughout much of a species range. As a species expands its range, however, at some point the predictive value of those signals will decline as that species invades beyond the limited domain over which environmental signals and underlying conditions, to which the species must be adapted, remain correlated with each other. In moving from northern to southern Europe, for example, plants encounter the fact that longer days becomes negatively, not positively, correlated with rainfall over the yearly cycle. The existence of discrete spatial autocorrelation domains for signals used to trigger adaptive plasticity, coupled with gene flow, may thus place important proximal and ultimate limits on a species' range.

Levin's treatment of genetic differentiation within mature species and their loss of cohesion through the formation of ecological and chromosomal races (Chapter 6) contains a number of pleasant surprises. Stimulating reviews are given of genetic differentiation during range expansion of diploid species in such genera as *Abutilon, Chenopodium,* and *Solidago.* His discussion of species decline and extinction in the following chapter is especially strong and draws heavily on the now-extensive literature on plant conservation biology.

But, as is the fashion with many population and conservation biologists, Levin gives inbreeding depression a lot of weight, and ecological factors promoting species decline are given rather short shrift. I feel this emphasis is somewhat misplaced, especially given Levin's avowed principle that ecology shapes all stages of the species cycle. As Levin himself mentions, one of the problems with assigning inbreeding depression a central role is that it creates selective pressures that tend to purge populations of the alleles (at least those of additive effect) that lead to inbreeding depression in the first place. Levin cites none of the papers by Rollins, Solbrig, or Lloyd on this subject and their crucial insight that species of *Leavenworthia* restricted to cedar glades atop especially small limestone outcrops have evolved small flowers with a high selfing rate, apparently because the loss of genetic variation via drift driven by ecological constraints has removed much of the genetic advantage of outcrossing. Where are the data showing that inbreeding depression does, in fact, drive the expected "death spiral" of a collapsing species, with reduced population size increasing inbreeding depression, leading to further reductions in population size? I worry that this process is overrated, given that a few large remaining populations can retain genetic variation, avoid inbreeding depression, and create new populations to replace smaller ones lost to inbreeding death spirals. Indeed, why don't most new populations, created by one or a few colonists, immediately succumb to inbreeding depression? And, if they do, how is it that plant species become established on recently emerged oceanic islands?

Levin prominently cites several studies showing a positive correlation between genetic variation and population size (pp. 135ff), but then an equal number of studies are just listed in which there is no such correlation; what are we to infer from this? Levin cites interesting data suggesting an Allee effect in *Banksia goodii,* but the question remains whether the observed decline in seed set in small populations is driven by inbreeding depression or pollinator limitation. Levin ascribes the decline of *Brighamia* (a rare, succulent lobeliad endemic to Hawaiian sea cliffs) to genetic factors, noting that seed set from open pollination is poor. Unmentioned is that *Brighamia* has highly fragrant, pale flowers with long corolla tubes, highly specialized for hawkmoth pollination and that the pollinator itself seems to have gone extinct! Cultivated plants of *Brighamia,* as well as those in the few remaining wild populations, set seed copiously when hand-pollinated, and the seeds germinate readily and grow into vigorous plants. The demographic meltdown of a heterostylous Japanese *Primula* studied by Washitani probably also involves the loss or increased rarity of its pollinator but one would never know this from Levin's account.

These instances are symptomatic of a widespread failing in the book: a fatal tendency to cite research only as short snippets of one or two sentences that bolster Levin's viewpoint and not to provide the detailed case studies that would allow us to understand and evaluate the important biology involved and convince ourselves of the validity of the argument being advanced. Perhaps this is an inevitable consequence of citing many hundreds of papers in such a slender book; if so, a longer and more thoughtful treatment would have been much preferred. But I have a nagging doubt that it might also represent only a passing acquaintance of the author with the papers cited.

I was unpleasantly surprised, for example, to find how research by my colleagues and myself on Hawaiian lobeliads was miscited or uncited, even though it is highly relevant to Levin's central themes. Givnish et al. (1995) provided a molecular phylogeny for *Cyanea*, the largest angiosperm genus endemic to the Hawaiian Islands, and discussed at length the processes that may have led to its remarkable diversification and subsequently high rate of extinction. We provided one of the first analyses of the ecological factors correlated with plant extinction, showing that extinction was correlated with initial rarity, ranges that were geographically and elevationally narrow, and highly specialized flowers with exceptionally long corolla tubes. Inexcusably, Levin ascribes these results to another author in a table he reprints from our own account! While mentioning our interest in taxon cycles in one sentence, he ignores completely our central conclusion: that the very factors that spawned high speciation rates and diversity in *Cyanea*—limited seed dispersal and long corolla tubes leading to numerous species with narrow ranges endemic to single islands and specialized on one or few pollinators—were also the ones that led to such a high rate of extinction. One could hardly have chosen to cite research that is more likely to crystallize Levin's themes regarding the ecological constraints of species' life cycles.

But Levin's treatment of ecological constraints often leaves much to be desired. For example, he cites some extremely interesting work by Thompson and Jones (1999) showing that the local extinction of plants in English vice-counties is correlated with human population density, not agriculture. Their message is accepted without comment, but really requires some further analysis to ensure that the correlations observed are not spurious. What, for example, are the correlates of low human population density in England? Almost surely, topographic relief is one, a factor that would keep people out and species in while allowing lots of land to be devoted to pasture. Levin's discussion of the ecological determinants of species decline and extinction misses a number of important papers. Leach and Givnish (1996), for example, showed that over the past three decades, Wisconsin prairie remnants have lost a disproportionate number of short, small-seeded, or N-fixing species, apparently as a consequence of fire suppression and/or increased atmospheric N deposition. Stocklin and Fischer (1999) found that grassland species with short-lived seeds were far more likely to go extinct; Jules and Rathcke (1999) showed that *Trillium ovatum* populations in fragmented forests were collapsing due to loss of pollinators and increased seed predation; and Harrison, Maron, and Huxel, (2000) documented an increased likelihood of local extinction of fugitive plant populations on serpentine seeps due to isolation from potential sources of colonists. Is inbreeding depression really a more important source of plant extinction than habitat destruction or, before these days of human hyperpopulation, than waves of newly evolved or invading diseases, herbivores, and competitors, or loss of pollinators, or changes in disturbance regimes?

Chapters 8 and 9 are relatively brief. The first discusses the mechanisms by which existing species might interfere with the rise of others. Levin states (p. 163) that:

> The challenge of the progenitor has been considered almost exclusively in terms of competitive interactions (Mayr 1963, . . .). However, progenitors may also affect the reproductive performance of their incipient neospecies. . . . The progenitor may also lead to the demise of incipient neospecies through genetic swamping.

This is entirely reasonable, but it was Mayr—not Levin—who originally emphasized the evolutionary importance of peripheral isolates because of the reproductive and genetic interference that the ancestral taxon could exert via swamping gene flow on incipient species. In analyzing the effects that selection among small, isolated populations of incipient species might have, Levin later states (p. 167):

> I contend that isolate selection, in addition to and perhaps rather than rapid speciation, has helped shape the barriers between peripheral neospecies and their progenitors.

This is quite reasonable, but didn't Verne Grant originally make this argument, in connection with the evolution of increased premating barriers in species of *Gilia* whose ranges abutted and could therefore hybridize? Speaking of hybridization, Levin raises the specter of compilospecies which, like the Borg, might threaten other species by crossing with them, assimilating their adaptive genetic variation, and then turning those adaptations against their original bearers. As Levin notes, recent work has raised the additional concern that, especially on islands, the introduction of weedy compilospecies that can cross with local, endemic relatives may seal the latter's doom by hybridizing their distinctiveness out of existence. Levin's final chapter recounts some of his early attempts to estimate species lifetimes for different groups of land plants; interesting, but I would have liked to have also seen citation and discussion of key paleobotanical papers by the likes of Leo Hickey, Jim Doyle, Andy Knoll, Peter Crane, and Pat

Herendeen, all of whom have helped revolutionize our view of the early evolution of land plants.

One central concern I had about the book as a whole was whether Levin had outlined an approach that is operational as presented. How can we determine, without resort to circular reasoning (or instead to the definitive phylogenetic and/or paleobotanical data, which are regrettably not presented) where in its life cycle a particular species is? If we did know this, would it tell us anything novel about where a species' ''evolutionary trajectory'' would likely carry it, independent of its current genetic makeup, its phenotypic adaptations, and its current constellation of natural enemies? It is not obvious, in other words, what the rate and direction of change of species' characteristics could possibly tell us that is significant and beyond the information contained in its current characteristics alone, whether there is some reality to evolutionary momentum/trajectory (shades of Osborn's orthogenesis!), whether there is some form of evolutionary hysteresis, or whether evolutionary responses to novel challenges are better envisioned as ricochets rather than trajectories. In any case, the progression of species through putative life stages surely is not as linear as that initially envisioned. Levin himself states (p. 159) that

> We cannot infer the trajectory of a species (i.e., whether it is contracting, expanding, or stationary) from the organization of its numbers in space at one point or a few points in time. Some rare species are neospecies in the process of expansion. Others are species expanding after a period of contraction.

The near or complete absence, at least in Levin's account, of data independently identifying where a species lies in its life cycle leads to a rampant multiplication of assumptions and at a minimum some distortions or outright errors. For example, his review of genetic variation in different species of *Polygonella* is baffling, partly because he tries to put them into ''declining species'' and ''expanding species'' boxes. Yet the narrowly distributed species in the southern United States are more genetically diverse than the widespread northern ones. The southern species appear to be more ancient relicts and the northern species recently derived, but this fact and the underlying phylogenetic data are not presented.

As this review indicates, I am skeptical that this book will make a lasting impression on plant evolutionary biology. The theoretical framework for the book as a whole is inadequately developed and explored, and conceptual bases for new predictions are lacking in many of the chapters. The entire enterprise is based on a questionable species concept and deeply flawed by a failure to incorporate modern phylogenetic and macroevolutionary data. The highly touted ecological perspective on plant evolution turns out, on closer examination, to be largely missing or poorly considered, as exemplified by the treatment of adaptive radiation, speciation itself, and the determinants of extinction. Dozens of technical terms are introduced without timely (or any) definition, and there are several instances in which claims made in chapter summaries are not substantiated by the previous treatment. In general, the reader is left with very little of the flavor (or, indeed, the meat!) of the very large number of studies catalogued, or a coherent view of what they collectively signify. Students in my laboratory refused to read or discuss the book after completing just a few chapters.

Yet, whatever the shortcomings of this book, the field of plant evolutionary biology itself is undergoing a radical and exciting transformation. While some indications of this transformation can be indeed be gleaned from Levin's book, particularly in the areas of plant population biology, population genetics, and conservation biology, I would advise interested students and professionals to read instead the fascinating, penetrating, and well-written accounts listed at the beginning of this review. They provide a tantalizing glimpse of an emerging new synthesis and represent the fruition of the work and dreams of Bailey, Babcock, Clausen, Lewis, Stebbins, Grant, Carlquist, and Raven.

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