

The Nature of Plant Species

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Organic diversity is divided into nodes and clusters of various sizes separated by relatively empty spaces. These clusters are assigned to categories in a taxonomic hierarchy that suggest their phylogenetic relationships. The most important category is that of species, which is the basic unit in taxonomy, evolutionary biology, and ecology. Yet the nature of species, especially in plants, is a matter of conjecture. Attempts have been made to empirically define species within a genetic context and to place species within the realm of a hypothesis that can be tested or has predictive value. Whereas this approach has met with some success

that species in practice do not comply with sets of prescribed rules. Claims about species as empirical entities are presented, followed by arguments to the contrary.

Species as Empirical Units

The species has had a special status as an evolutionary unit because it is thought to be more natural than higher categories and more amenable to definition and empirical demonstration (3-5). Specifically, there are three features that allegedly make the species a unique evo-

Summary. The species concept is a central tenet of biological diversity. Attempts to describe diversity have led to empirical concepts of species based on assumptions found wanting for plants. Plant species lack reality, cohesion, independence, and simple evolutionary or ecological roles. The concept of species for plant taxonomists and evolutionists can only serve as a tool for characterizing diversity in a mentally satisfying way. Diversity is idiosyncratic. It is impossible to reconcile idiosyncrasy with preconceived ideas of diversity. The search for hidden likenesses is unlikely to yield a unifying species concept. The concept that is most operational and utilitarian for plants is a mental abstraction which orders clusters of diversity in multidimensional character space.

when applied to animals, the characteristics and diversity of higher plant genetic systems and reproductive modes preclude the application of a universal plant species concept (1). Davis and Heywood (2) argue cogently that absolute experimental definitions of "species" are impossible. If the plant species defies empirical demonstration, we are faced with a series of pivotal questions: Is the plant species a natural unit of evolution, or is it a grouping category embracing diverse assemblages with few genetic or ecological attributes in common? In either case, are species real or are they mental constructs? Do empirical concepts of species reflect the organization of diversity as it actually exists? Do experimental concepts order diversity not by edict but in fact? The purpose of this article is to show that plant species are utilitarian mental constructs, and

lutionary unit. The first is their apparent reality. Mayr (4) states "that species are real objective units, because the delimitation of each species is definite, and not open to argument except in border-line cases." This idea is further developed in an essay on the biological meaning of species where Mayr (6) states, "*Species are the real units of evolution*, they are the entities which specialize, become adapted, or which shift their adaptation. And speciation, the production of new gene complexes capable of ecological shifts, is the method by which evolution advances. The species truly is the keystone of evolution. . . ." The species "receives its reality from the historically evolved shared information content of its gene pool" (7).

The second cogent feature of species is the apparent integration of their populations. According to Löve (8), "Each

species is a reproductive community. It consists of populations each of which is an expression of an integrated gene pool. . . ." Dobzhansky *et al.* (9) observe that "A sexual species is a reproductive community, all members of which are connected by ties of mating, parentage, and common descent. The reproductive community has a common gene pool. Possession of a common gene pool makes a sexual outbreeding species an inclusive Mendelian population. More precisely, a species is an array of subordinate Mendelian populations interconnected by regular or occasional gene flow. The Mendelian population is a form of supraindividual integration." White (10) asserts that "It cannot be emphasized too strongly that every species is at the same time a reproductive community, a gene pool, and a genetic system." This idea is complemented by Dobzhansky *et al.* (9), who stated that "A species is an array of related gene combinations that occupy [an] adaptive peak. . . . The summit of the peak is held by the genetic 'elite.' The question of why there should be species can thus be answered: because there are many adaptive peaks."

The third feature of species is their apparent independence. As noted by Dobzhansky (11), species represent the stage of evolutionary divergence at which the once actually or potentially interbreeding population systems become segregated into systems incapable of interbreeding, and thus capable of pursuing independent avenues of adaptation. Löve (12) contends that the mechanisms leading to the genetic isolation of populations are the mechanism of speciation in the strictest sense.

The notions of reality, cohesion, and independence also are present in ecologically oriented concepts of species. Simpson (13) proposed that "An evolutionary species is a lineage evolving separately from others and with its own unitary evolutionary role and tendencies (or niche space)." This concept has been modified into the ecological species concept by Van Valen (14) as follows: "A species is a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range." An adaptive zone is considered some part of the resource space plus parasites and predators encountered.

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The Reality of Species

The reality of species is a matter of conjecture. Locke (15), in his *Essay Concerning Human Understanding*, wrote as follows: “*genera and species . . . depend on collections of ideas as man have made, and not on the real nature of things . . . our distinct species are nothing but distinct complex ideas, with distinct names annexed to them.*” Later, in the *Origin of Species* Darwin (16) concurs with Locke. He wrote, “I look at the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other, and it does not essentially differ from the term variety which is given to less distinct and more fluctuating forms.”

The contemporary principles of population biology and taxonomy do not make the species concept more sanguine. Ehrlich and Holm (17) state that “the idea of good species . . . is a generality without foundation—an artifact of the procedures of taxonomy. These procedures require that distinct clusters be found and assigned to some level in a hierarchy—subspecies, species . . . and so on.” In turn the taxonomic system itself communicates little about the organism being discussed, although it appears to communicate a great deal. Raven *et al.* (18) conclude that “Our system of names appears to achieve a reality which it does not in fact possess.” Apparent reality not only is conferred by the system but also is the result of formulating a satisfying mental organization of diversity (19).

Spurway (20) and Haldane (21) suggest that our concept of a species may result from the structure of our language and the structure of our brain. Language expresses a specifically human way of analyzing our experience of the external world (22). Correlatively, structuralist philosophy holds that human behavior and perception are determined by our subconscious penchant to divide an assemblage of objects into clusters and form an abstract generalized concept of each resulting assemblage (23). Bronowski and Bellugi (22) contend that the search for structural relationships in the environment characterizes the human mind and is equivalent to the procedure of generalization or inductive inference. For humans the environment has meaning only when its components can be interrelated in a predictive structure. We try to make sense out of nonsense and put the world into some perspective which has order and harmony.

Species Integration by Gene Flow

The assumptions that plant species are Mendelian populations integrated by the bonds of mating do not have substantive support. This point was made explicitly by Ehrlich and Raven (24). Their idea of restricted gene flow among plant populations was well substantiated in a recent review (25) and is consistent with subsequent observations.

A massive literature on the dispersion of particulate matter from aerial sources (26) provides a solid framework for understanding and predicting the dispersion of wind-borne pollen. As with other airborne particulates, the deposition schedule of pollen on stigmas over distance depends on the vagaries of the atmosphere, the size and mass of the pollen, the height of pollen release, the size and shape of the population from which the pollen is released, and the nature of the vegetation through which the pollen must pass. Empirical studies on crop plants show that pollen dispersal beyond 1000 meters is very rare, and at those distances extraneous pollen would constitute only a minute fraction of the pollen cloud over another population (25). Similar results are reported by Raynor and associates (27) and others (25) on wind-pollinated native plants. Pollen dispersion data are consistent with data and theory on wind-borne particulates of pollen size.

Pollen may be transported hundreds of kilometers and be airborne for days. However, such pollen may not be viable. Pollens of corn, wheat, barley, and other grasses typically do not survive for more than 24 hours (28). Thus, long-distance pollen transport for herbs may be less important than anecdotal observations would suggest. Moreover, we cannot assume that the competitive ability of “old” pollen is the same as “new” pollen; probably there is some decay in performance over time.

Pollen dispersal by animals is restricted, as would be expected from optimal foraging theory (29). Interplant flights usually take place between a plant and one of its near neighbors, except when resources have been locally depleted. The foraging area of single animals tends to be rather narrow over time. Site constancy is well documented in some bees, butterflies, and hummingbirds, lasting from several hours to several days (30). Time may also limit long-distance pollen flow. Kraai (31) studied several honey bee-pollinated crops and ornamentals and found that the bees, after being enclosed for 12 hours, no longer carried

germinable pollen on them. Pollen in deciduous fruits, alfalfa, guava, and cacao typically survives for only a few hours under natural conditions (28).

In this discussion of pollen flow obligate outbreeding is assumed. With self-compatibility, the probability of pollen from other populations being effective is inversely proportional to the level of self-fertilization, which would be equivalent to zero-distance pollen flow. Similarly with partial asexual reproduction, the significance of extraneous pollen grains is inversely proportional to the level of asexual reproduction.

Actual gene flow via pollen between populations of insect- or wind-pollinated crops typically is over short distances and is highly leptokurtic (25). The minimal isolation distances for the maintenance of varietal purity as recommended by the Association of Official Seed Certifying Agencies (32) are less than 100 meters for most species and less than 1000 meters for all included in their listing. Isolation distances are less for self-compatible species than obligate outcrossers. Juxtaposed populations may hybridize freely, but as distance increases the level of hybridization declines sharply (25).

Seed dispersal seems to be of little importance for multipopulation cohesion. Seeds most often are dispersed by wind, animals, or by the explosive dehiscence of the fruit. The distances over which wind-borne seeds and fruits travel depends on their settling rate (or terminal velocity), the height and area of the source, and turbulence and wind velocity.

Burrows (33) and Sheldon and Burrows (34) have shown that the maximum distance that many Compositae achenes travel would be less than 10 meters in steady wind. The distances might be ten- or a hundredfold greater given sufficient turbulence, but still a short distance. Because of their great height, trees with wind-dispersed fruits have wider dispersal radii than herbs, but dispersal beyond 200 meters is indeed rare (35). The aerodynamic properties of the samaras and single-winged fruits of angiosperm trees will explain why winged fruits do *not* disperse very far beyond the parent trees (36). The movement of dust seeds follows the aerial mechanics of a small spherical particle (36). Thus, we may surmise that dust seeds only rarely will be carried beyond 500 meters. Explosive seed dispersal by herbs yield maximum distances less than 10 meters (25). However, the seeds of some trees may be dispersed as far as 45 meters

from the parent (37). There is a strong positive correlation between the height of plants of various species and the distance that their seeds are shot.

In many species occasional long-distance seed dispersal is accomplished by animals that either eat the seeds or carry them externally (38). Birds are important in the long-distance dispersal of seeds; yet the dispersal schedules may be highly leptokurtic, with most seeds remaining in the vicinity of the seed source. Howe (39) reports that after feeding on the seeds of certain tropical forest trees some birds process arils and regurgitate seeds while sitting in the canopy from 20 to 200 meters from the seed source; other birds regurgitate most seeds while in the tree crowns where harvesting occurred.

The distances over which seeds are carried internally or externally by mammals are not well understood. Granivorous mammals seem to have small home ranges and rarely carry seeds more than 100 meters from seed sources (40). Larger mammals that graze may be effective in the long-distance transport of seed, but we only have anecdotal records of internal passage times of seeds for species whose foraging ranges are known. Bullock and Primack (41) addressed the problem of external seed transport experimentally; they used a cloth-covered surface and carried it in a straight line through various types of vegetation. The mean transport distance was more than 100 meters with some exceeding 2 kilometers. These measured distances were based on the assumption that the dispersing agent moves along a straight line. For a realistic foraging pattern the actual distances would be much less because of the nonlinear route of the transporting agent.

The fact that species colonize areas well beyond their previous ranges bespeaks of long-distance seed dispersal. However, colonization and gene flow via seed cannot be equated, since in colonization there is no large indigenous seed population. The converse is true with gene flow. In summary, the frequency of long-distance seed exchange between populations is poorly understood, but it seems to be very low.

The idea that plant species are Mendelian populations wedded by the bonds of mating is most difficult to justify given our knowledge about gene flow. Indeed a contrary viewpoint is supported. Populations separated by several kilometers may rarely, if ever, exchange genes and as such may evolve independently in the absence of strong or even weak selective

differentials. If local populations exchange genes, the level of exchange will vary in time and space as a function of interpopulation distance and size. The Mendelian population is a fluid entity and is, of necessity, not consistent with variation patterns in space or time.

Species and Reproductive Isolation

Consider next the idea of defining or delimiting species by reproductive isolating mechanisms. It is important to recognize that isolating mechanisms do not exist as properties of single species or single populations. A reciprocal translocation, or a particular corolla color do not of themselves constitute isolating mechanisms; they become so only when related populations differ in these regards. Essentially, isolating mechanisms reside at the hypothetical interface between populations and are not independent of that interface. Isolating mechanisms arise from the incongruities in the genomes that we chose to pair. Isolating mechanisms are not the cause of divergent evolution any more than isolation by distance is the cause of diversent evolution. Isolating mechanisms are not essential for divergence any more than allopatry is essential for divergence.

The origin of species often is defined by the appearance of reproductive isolating mechanisms (42). If speciation is contingent on well-developed isolating mechanisms, then the process is divorced from divergent evolution, because divergence is not dependent upon reproductive isolation. If speciation is contingent on the presence of isolating mechanisms, then speciation is capricious, because isolating mechanisms generally arise as incidental by-products of divergent evolution. But where does this leave us, if the species is the keystone of evolution (6)? How do we get from one adaptive peak to another, from one resource space to another, if speciation is incidental to the adaptive process? Does the transition occur subsequent to speciation or do populations move from one adaptive peak (resource space) to another before the barriers emerge?

Although isolating barriers retard gene exchange between populations, the effect may be no different from isolation by distance. In the absence of selection, reproductive barriers function as "distance extenders," and are not qualitatively different in effect from distance per se. The effective distance that the

barriers impose between populations is a function of collective barrier strength. Weak barriers may retard gene exchange between juxtaposed populations to the same extent as a distance of 100 meters between populations. Strong barriers may impose an effective distance of 100 meters or more. It follows that gene exchange between partially reproductively isolated populations that are intermixed or closely adjacent may be greater than that between populations that are not reproductively isolated but are separated by considerable distance. It also follows that within an array of populations there may be a lack of correspondence between the location of phenetic and genetic transitions, and reproductive barriers. These expectations have empirical support (43). Reproductive barriers are differences that effect genetic or chromosomal incompatibilities between populations. They do not of necessity delimit or correspond to phenetic discontinuities upon which utilitarian taxonomies are based.

Species as Evolutionary and Adaptive Units

The pattern of differentiation in a multitude of species is in close accord with the pattern of environment which may vary manifestly across the range of a species (44). This relationship seems to belie the notion that all conspecific populations occupy the same adaptive peak or play the same evolutionary role. Do plants with multiple adaptations for heavy metal tolerance (45) occupy the same adaptive peak or do they have the same evolutionary role as related plants growing on normal soils? Similarly, do populations from coastal California have the same evolutionary role as conspecific populations in the alpine zone of the Sierra Nevada Range, which differ strikingly in many single and multigenic characters (46)?

If populations with common adaptations are adaptive peaks, then species may best be viewed as collections of multiple adaptive peaks with continuity between the peaks. Genera and families also meet criteria of multiple adaptive peaks. Wright (47) indicated that panmictic species could occupy single adaptive peaks. However, with restricted gene flow as in many plant assemblages, especially with selfing, he shows that a species might occupy multiple selective peaks. With small species size and close inbreeding, a species might reside between peaks rather than on them.

Conclusions

As with all theoretical concepts, species concepts bear within themselves the character of instruments. In the final analysis they are only tools that are fashioned for characterizing organic diversity. Focusing on the tools draws our attention from the organisms. As enunciated by Raven (48) "the preoccupation with . . . the recognition of taxonomic units may often tend to conceal the facts upon which such classifications are based. . . . The species concept, lacking a universal definition, has very little predictive value, but provides a kind of false assurance that they have a number of key biological properties." For this reason, he argues that species concepts may lead to the loss of information and distort out perception of natural populations.

Systematic and evolutionary botany are sciences of idiosyncrasy. Whereas the processes of plant evolution are universal, the products are highly idiosyncratic owing to inherent differences in their genetic systems, sociology, and selection pressures. Instead of searching for unity in hidden likenesses, the ambiguity of nature would best be dealt with group by group. As so aptly stated by Cronquist (19), "Ultimately, the taxonomist must produce a treatment that appeals to the mind as the best conceptual organization of the diversity that exists in nature."

We remain faced with the critical problem of why groups of populations appear similar to one another, which gives the impression of contemporary integration, or conspicuous order. As noted by Levi-Strauss (49), we "detotalize" individuals and concentrate on the single characters or character ensembles abstracted from whole organisms. Making assemblages or populations is done by classifying organisms with similar properties, all details being potentially significant. Therefore, if we recognize assemblages that differ in a few conspicuous traits but have many in common, we would encompass races or subspecies. If we ignore what we deem minor variation and concentrate on another set of shared characters, we would encompass the taxonomic species. If we concentrate on a more conservative set of characters, we would encompass the genus. Accordingly, part of the order we perceive is the product of our choosing.

Given that we choose the characters that delimit groups, the problem still re-

mains as to why groups are rather homogenous. At the species level, gene flow, stabilizing selection, canalizing selection, developmental homeostasis, or negative correlations between fitness characters may be involved to various degrees. Whereas these processes undoubtedly are important, homogeneity also may be the product of so-called "no-change." Given that populations have a common ancestry and share a specific habitat space, expansion from the region of origin need not be accompanied by conspicuous change provided that the populations spread into habitats to which they are adapted and enter easily. If they migrate along paths of little resistance, as a river moves within established channels, the selective pressures bringing geographical differentiation would be small, and homogeneity would be the result.

Although we may recognize the prime factors responsible for interpopulation similarity, we have not been able to estimate their absolute or relative importance. Yet it is apparent that at a given taxonomic rank, the basis for interpopulation similarity need not be the same in kind or importance. Similar products need not derive from the same processes. For this reason, we should avoid promulgating species interpretations founded upon a common underlying process or interaction. These species are formulated by edict. Species interpretations based on the products of evolution are not shackled with implicit or explicit assumptions of causation; they address diversity and idiosyncrasy in an operational and utilitarian manner. We create and amend species interpretations until we have a mentally satisfying organization, and this procedure works quite well for most assemblages of populations.

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