The Driving Force: Species Concepts and Ecology
Author(s): Lennart Andersson
Source: *Taxon*, Vol. 39, No. 3 (Aug., 1990), pp. 375-382
Published by:
Stable URL: http://www.jstor.org/stable/1223084
Accessed: 02/01/2011 20:14

http://www.jstor.org

THE DRIVING FORCE: SPECIES CONCEPTS AND ECOLOGY

Lennart Andersson[1]

Summary

In both folk taxonomy and science, the idea of species is based on the observation that phenotypic variation is discrete and not continuous. The definition of the species category, the "what," must therefore be restricted to these empirically demonstrable facts. To avoid circularity, concepts about the biological nature of species, the "whys," must be kept separate from the criteria by which individual species are circumscribed. Such ideas are models and can only be judged in terms of their capacity to bring observations into a meaningful context. The Biological Species Concept (BSC), the Evolutionary Species Concept (EvSC) and the Ecological Species Concept (EcSC) are models, not definitions. The BSC has its principal flaw in its inability to deal with uniparentally reproducing organisms. It fails to identify the driving force of speciation. It therefore fails to predict diversity and to explain why different species have different reproductive strategies. The EvSC fails to explain why different lineages are phenetically different. It fails, therefore, to explain why species arise, and why there are differences in diversity and reproductive strategies. The EcSC has the potential to make a direct connection between environment and phenetic variation patterns. It provides a useful conceptual framework for experimentation and observation at the interface between taxonomy and ecology and has the potential to explain on a universal basis variation in diversity and reproductive patterns. In some taxonomically difficult cases it also sheds light on the nature of variation patterns and might therefore help in taxonomic judgment where the BSC is conceptually inapplicable and the EvSC fails to provide useful concepts.

Introduction

The literature on species concepts is vast, dispersed, and varied. The only thing generally agreed upon is that variation in phenetic parameters is not continuous and that character states are not combined randomly. Mostly, this is taken to mean that species are real and not mere artifacts created by the minds of observers. Totally different views exist (e.g., Levin, 1979), but are minority opinions. Compromise opinions, like those of Cronquist (1988) and Davis and Heywood (1963), allow for a gradual scale from quite arbitrary to fully objective species. Most practicing taxonomists take for granted that species can be recognized by inspection, though inspection sometimes has to be extremely close.

Species may be visualized as clusters of individuals in a multidimensional space, where each dimension marks a character axis. Each cluster is separated from other clusters by empty interspaces. Consequently, speciation is a compartmentalization of the total character hyperspace and species definitions ("descriptions") circumscribe, in an oblique way, such compartments. When the species is defined as the category of clusters that are inwardly continuous and outwardly discrete, that is a purely phenetic species concept (PSC). It is the most common basis in practical taxonomy, irrespective of whether the taxonomist is aware of it or not. Its most apposite formulation is probably that of Cronquist (1978), going back to an older one proposed by DuRietz (1930). Cronquist defines species as "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means."

The PSC is a purely operational concept, being based entirely on empirically demonstrable facts. Species concepts that include criteria concerning the genesis or function of species are to be viewed as hypotheses about the "true" or "biological" nature of species.

[1] University of Göteborg, Department of Systematic Botany, Carl Skottsbergs Gata 22, S-413 19 Göteborg, Sweden.

The object of such hypotheses is not to define what species are but to explain why phenetic variation is compartmentalized or how compartmentalization comes about or is maintained. They are models, and as such they can be judged only by their capacity to serve in meaningful generalization. There are three partly overlapping schools of thought in this field: 1) the biological (or reproductive) species concept (BSC); 2) the evolutionary species concept (EvSC), and 3) the ecological species concept (EcSC).

As discussed by Cronquist (1978, 1988), Raven (1980), Grant (1981), Jonsell (1984), and others, the BSC fails to provide a unifying species concept for all organisms. The evasion that apomictic and autogamous organisms form "pseudospecies" has not proven palatable to most taxonomists. Phenotypic compartmentalization is a universal phenomenon and it may justly be supposed that it is effected by a universal cause.

The EvSC seems to be the concept favored by the largest number of contemporary plant taxonomists. Nonetheless, as shown by Lidén and Oxelman (1989), it leads to insurmountable contradictions because it confuses process and pattern. Furthermore, it is inoperative, because the decisive criterion, lineage affiliation, cannot be empirically demonstrated. Advocates of the EvSC certainly take it for granted that lineage affiliation can be determined from phenotypic expression, but there are no a priori reasons to do so. Wiley (1981), the most eloquent protagonist of the EvSC is quite vague on this point.

Under the EcSC, species are defined as lineages (or sets of closely related lineages) occupying minimally different adaptive zones (Van Valen, 1976). Species are thus thought to become, and remain, different because of differential selection. Common descent is thought to be the source of similarities, and reproductive strategies are viewed as adaptive character sets comparable to other such sets. As a corollary, it follows that compartments of character space correspond to compartments of eco-space, i.e., distinct niches or adaptive zones.

In my view, only the EcSC has the potential to explain speciation on a basis common to all organisms. It also has the potential to become a theoretical framework for useful and testable hypotheses about general laws of diversity in the organism world, and to provide taxonomy with new practicable criteria.

The purpose of this paper is to explore the potential of the EcSC in taxonomy and its consequences when using taxonomic data in general biological theories.

Ecology and Species Concepts

The idea that ecology plays some part in speciation is present, implicitly or explicitly, in most species concepts. Even workers who advocate a strict PSC may have such ideas as an implicit, underlying framework. Cronquist (1988), for example, adheres to a wholly operational PSC but still accepts that species may, at least sometimes, correspond to ecological units. He does, however, admit that there may be other possibilities, including, in some cases, total arbitrariness of individual species.

While classical BSC definitions do not use other criteria than presence of reproductive barriers, the redefinition of Mayr (1982) states that possession of a proper ecological niche is a characteristic of biological species (BSPs). Niche separation is viewed, in fact, as the driving force in speciation: reproductive barriers exist because they guarantee the integrity of adaptive gene complexes. Still, however, the possession of a common gene pool is viewed as the fundamental, defining, property of BSPs.

Simpson's (1961) and Wiley's (1978, 1981) definitions of the EvSC list explicitly the possession of a proper ecological niche (or equivalent) among the properties defining evolutionary species (EvSPs). Still, selection is viewed as subordinate to genealogy, and Wiley (1978) states, without corroboration, that "it is possible for two species to share essentially the same niche within the same range." Unfortunately, it is not absolutely clear whether Wiley means that individual EvSPs are defined only by their genealogy, or if they are also phenetically distinct. It appears that his definition only requires that lineages are repro-

ductively isolated. In his further discussions, however, he takes for granted that lineages can be identified by inspection. Hence, it is not clear what is meant by "evolutionary tendencies" and "evolutionary role."

The first clear and straightforward formulation of an EcSC is that by Van Valen (1976), who places primary emphasis on selection and niche adaptation and regards other factors, such as genetics and reproduction, as secondary. This is clear from the provocative dicta given as his "underlying framework": 1) "genes are of minor importance in evolution and should be considered there in nearly the same degree (if not for the same reasons) as other molecules"; 2) "control of evolution is largely by ecology and constraints of individual development"; and 3) "selection acts primarily on phenotypes, which are the building-blocks of communities." Van Valen (1976) defines a species as 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 defined as "some part of the resource space together with whatever predation and parasitism occurs on the group considered." Adaptive zone is thus a wider concept than niche (as defined by, e.g., Silvertown, 1982). Views similar to those of Van Valen's have been reached independently by, among others, Raven (1978, 1980).

The EcSC as such has not been much discussed in the 14 years since the publication of Van Valen's article. Wiley (1978) says that Van Valen's discussion "[has] merit but it is my opinion that such concepts lead to underestimation of the rates of extinction due to interspecific competition." Jonsell (1984) does not discuss Van Valen's concept in detail, simply stating that he finds it "interesting" but "no more operational than the [BSC]."

One cornerstone, with which the EcSC stands or falls, is, of course, whether plants do really need something conceptually similar to niches or adaptive zones. This has been flatly denied by a number of authors, e.g., Connell (1978) and Silvertown and Law (1987). Some of this controversy stems from a narrow niche concept, where factors related to establishment in naturally disturbed vegetation are excluded *a priori* as niche axes (so by Connell). Other authors, like Silvertown and Law, maintain that in some habitats, such as the tropical rainforest, too many closely related species coexist to make niche separation credible. This latter line of argument is largely based on a misconception of what rainforest vegetation is really like. Firstly, α- and β-diversity are confused. As shown by Gentry (1988), there is a strong tendency to edaphic specialization in tropical vegetation and a low degree of overlap between samples from different soil types. Hence, high diversity in tropical rainforests is largely high β-diversity. This supports rather than discredits the idea that niche separation occurs. Secondly, species growing together on homogeneous hectare plots are mainly not congenerics. In a recent study by Balslev et al. (1987), the most diverse genus on a very species-rich hectare plot (*Guarea*) was represented by only nine species out of a total of 228 tree species over 10 cm dbh. This makes only 2.5% of the tree species and much less of the total flora. Congenerics coexisting in limited and edaphically homogeneous areas are, in my experience, never the closest relatives in the genus. To the contrary, it has been demonstrated in some studies that closely related congenerics, when sympatric on a geographical scale, tend to differ conspicuously in habitat preferences (e.g., Burger, 1974; Berry, 1982). The view that plants do not need niches seems poorly founded.

Hengeveld (1988), criticizing Mayr's (1982) redefinition of the BSC, argues that niches are not easily defined, nor is the process of niche differentiation well understood from the ecological and ecophysiological points of view. He argues that niches are not identifiable independently of the organisms that occupy them and reaches the conclusion that "niche differentiation and identity is often unknown or much in dispute and should be considered essentialistic in the realm of biology." Along another line of reasoning, where he denies the existence of a universal nature of species, Levin (1979) reaches the conclusion that "similar products need not derive from the same process. For this reason we should avoid promulgating species interpretations founded upon a common underlying process or in-

teraction. Species interpretations based on the products of evolution are not shackled with implicit or explicit assumptions of causation."

In my view, the following generalizations could be made: 1) Individual species can only be defined in a phenetic context, i.e., as (persistently) discrete compartments of character space. The species category is thus a category of patterns, viz., the smallest pattern units that are inwardly continuous and outwardly discrete. It is immaterial to this definition that pattern units (character hypervolumes) may have different shapes, i.e., that variation ranges may be wide or narrow, uni-, bi- or multi-modal, etc. Nor is the relationship of character distribution to geography (clinal or random) of any consequence.

2) Selection and adaptation to different adaptive zones is the main reason why compartmentalization occurs: it pays to specialize. Because compartmentalization is effected by selective pressure, it is to be expected that the shape of the character hypervolume is part of the adaptive character complex of a species, i.e., variation pattern, and thus reproductive pattern, is an adaptive character in itself. One should, therefore, expect that some laws could be formulated that express the relationship between habitat parameters and the shape of the character hypervolumes, i.e., the variation pattern.

3) The means by which compartmentalization is effected varies from group to group; the pathways to speciation cannot be generalized, only systematized. The only generalization is that when an "empty" niche is available, it will be filled by that one out of a multitude of initial competitors who finds the least costly (complicated) way to specialize.

4) It is generally permissible to assume that organisms belonging to the same phenetic hyperspace cluster belong to the same genealogical lineage. The complexity of a specific adaptive character set is such that it is highly unlikely that coordinated parallelism would occur in all characters.

5) The limits of realized niches are set by interspecific competition. Therefore, species cannot be defined, only "explained," by the adaptive zones they inhabit. It should be expected, however, that discrete species occupy distinct niches. In taxonomic practice, therefore, demonstrable niche differences could be used as a secondary criterion by which to decide whether or not to recognize a morphotype otherwise difficult to assess.

Some Consequences of the EcSC

Species in the time dimension. — There is an inherent conflict between the conceptual frameworks of pattern and process. Nevertheless, the conclusion that "attempts to apply temporal aspects to taxa, including species, are doomed to lead to unsolvable paradoxes" (Lidén and Oxelman, 1989) is not justified. Character space has no time dimension. Any organism from whatever point on the time axis can be placed in the same character space. On the other hand, compartments of character space can only be defined arbitrarily or with reference to the objects present there. In the time dimension, therefore, species can only be defined arbitrarily or with reference to compartment limits set by contemporary organisms, or organisms from some other, arbitrarily selected transect of time-character space. Consequently, ancient organisms belong to the same species as present ones as long as they fall within the same character space compartment. Species defined under the PSC do have time extension, and it is an empirical question, however rarely approachable, to decide how far they extend. From the standpoint of the PSC, anagenesis and cladogenesis are equivalent and Hennig's (1966) dictum that species go extinct at branching points is senseless.

Under the EcSC it is to be expected that stasis persists as long as external factors, biotic and abiotic, remain essentially the same. Conversely, speciation is to be expected in times of environmental change. This is actually the implicit basis of much biohistorical theorizing, but the basic condition, the ecological nature of species, is rarely made explicit. Often, I think, this is because this condition is felt to be trivial. That it is not is demonstrated by

the considerable problems involved in relating differences in the speed of evolutionary change to the models of the BSC and EvSC.

Ecological criteria in taxonomic judgment. —Ecological criteria cannot be used to define (circumscribe) individual species. For reasons discussed above, this would lead to circularity. It seems justifiable, however, to use demonstrable habitat differences as criteria by which to decide whether or not to give taxonomic recognition to a morphotype for which phenetic criteria are not conclusive. The practical consequences in taxonomy may be significant, as the following examples intend to show.

The agamospermous genus *Taraxacum* is represented in Scandinavia by more than a thousand constant and minimally different morphotypes ("microspecies"). In the framework of a barren PSC this is a difficult case, because these morphotypes are both consistently and (nearly) persistently different. Whether they are recognizable by "ordinary means" is largely a matter of taste and training. Under the EvSC they are doubtless species, as each morphotype represents a separate lineage.

Under the EcSC the case looks different, and more promising. According to Jonsell and Jonsell (1984) there are seven morphologically fairly discrete groups of microspecies and ecological characteristics are essentially found at this group level. The *T. erythrospermum* and *T. obliquum* groups grow in dry grassy vegetation and on eroded sand and are morphologically similar. The morphologically isolated *T. palustre* group grows on more or less naked soil in the inundation zone of shores and pool margins. The somewhat isolated *T. ceratophorum* group, and the closely interrelated *T. boreigenum, T. croceum,* and *T. spectabile* groups grow in meadows, mainly in the boreal and alpine zones. The *T. vulgare* group, by far the one richest in "microspecies," is confined to manmade habitats such as lawns, pastures, wastelands, etc. It appears to me that the number of EcSPs among Scandinavian Taraxaca is less than ten, perhaps somewhere around five. Rather than spending more time and energy on the trifles of morphological variation, which has been thoroughly examined and found hopeless, one should make an effort to get hard data (not anecdotal, as above) relating morphological variation to habitat parameters.

Maranta subgen. *Maranta* is a group of predominantly autogamous species. Traditionally (e.g., Schumann, 1902) about five species have been recognized, most of them vaguely circumscribed. In a recent revision (Andersson, 1986) I raised the number to 16. As far as data are available, these species seem to be well characterized in habitat terms. Species that are similar with respect to habitat preferences are largely or wholly allopatric. *Maranta arundinacea s. str.* has a circum-Caribbean distribution and is confined to dry tropical forests; the closely related *M. linearis* grows in inland savannas on the Río Orinoco-Rio Negro watershed, and *M. amplifolia* in edaphic (white sand) savannas throughout the Amazon region. These three species form a morphologically well characterized group. Another such group is formed by *M. amazonica, M. divaricata, M. gibba, M. protracta,* and *M. rupicola.* Of these, *M. gibba* and *M. protracta* seem to have similar habitat requirements (seasonal evergreen forest on latosol), but are allopatric. *Maranta amazonica* grows on latosol in pluvial rainforest. *Maranta rupicola* grows on rock savannas and in coastal scrub forest ("restinga") on sandy soils and is partly sympatric geographically with *M. protracta* and *M. divaricata. Maranta divaricata* grows in dry, scrubby, evergreen forest close to the sea on so-called morros (granitic outcrops) along the southeastern coast of Brazil. Other species are too poorly known to be characterized ecologically. Nevertheless, even the scanty and imprecise data presently available add evidence in support of my treatment. More detailed and harder data are certainly to be desired.

Agrostis canina (2n = 14) and *A. vinealis* (=*A. stricta,* 2n = 28) differ not only in chromosome number, but also, and strikingly, in shoot structure. *Agrostis canina* produces thin, whitish soboles but no stolons, whereas *A. vinealis* produces stolons but no soboles.

Although the two taxa have been recognized as varieties or subspecies since the early 1800's and although the difference in habitat preferences have been known for very long, it is only recently that they have been generally recognized at the specific level (Widén, 1971). Certainly, this is because of great similarity in reproductive structures and ligule shape, the two characters most strongly emphasized in the genus. In actual fact, they are a good example of a small polyploid complex where ecological data favour one taxonomic treatment at the expense of a competing one.

The taxonomic treatment of vicarious morphotypes is a field where taxonomists have often fumbled in vain for rigid criteria (see Hedberg, 1958). It appears that the EcSC would provide an extra argument to give specific status in doubtful cases to variants that have demonstrably different habitat requirements. The reverse is not true, however. In cases where ecological differentiation is not apparent, one is stuck with the PSC. On the other hand, the BSC does not offer a conceptually useful framework at all, and the EvSC does not give anything in addition to the PSC, except that under its most extreme variants, all allopatric populations would have to be treated as distinct species. The EcSC offers at least a conceptual framework where a new, independent set of empirical data may be fitted in.

Hybridization and introgression. — There is a considerable body of accumulated evidence indicating that hybridization plays an important role in speciation (e.g., Stace, 1975; Raven, 1980). Under the BSC and its corollary, the allopatric speciation model (defended by Mayr as late as 1988), hybrid speciation appears more an anomaly than a normal pathway. Also the EvSC fails to provide a conceptually useful framework to explain the phenomenon. Under the EcSC, with its primary emphasis on adaptation and selection, the adaptive value of a gene or gene complex is the important thing, while the source is immaterial. When new habitats arise, be it by the formation of new land or by major climatic change, the newly formed habitats will be invaded by those organisms that find the least costly way to achieve new adaptive gene combinations. The least costly way will probably often be to borrow genes from some other species by way of introgression, or by hybridization coupled with agamospermy or polyploidy.

There are several examples rather clearly indicating that the establishment of amphiploid species in Europe was related to profound habitat changes caused by Pleistocene glaciations. Thus, the amphiploid *Poa annua* seems to have arisen at the southern edge of the icesheet at glacial maximum (Tutin, 1957). *Saxifraga osloensis,* derived from the hybrid *S. ad-scendens* × *tridactylites,* is still confined to the glacial regression zone across central Fennoscandia (Knaben, 1954).

As pointed out by Van Valen (1976), the complicated variation pattern in North American oaks is probably best understood as ongoing introgression. Van Valen argues that this state is adaptive in giving all species of the comparium access to genes that are adaptive only in some situations and not in others. Though less intensively studied from the biosystematic point of view, the genus *Salix* probably offers a close parallel from the Old World. Van Valen's (1976) interpretation of the situation in North American oaks is nicely supplemented by the following, more general, statement by Raven (1980): ". . . no particular pattern in nature can logically be regarded as the precursor of any other. . . . ecotypes, races, subspecies, and 'semispecies' cannot be regarded as stages in the evolution of species." Reproductive systems, and hence variation patterns, are adaptive features in themselves.

Diversity. — The fact that some habitats are much more diverse than others is extremely puzzling under the BSC and EvSC. Based upon these concepts (and often on no explicit concepts at all), a number of totally untenable ideas have been put forward. Tropical lowland rainforests have been viewed as evolutionary museums, high diversity being the effect of long evolutionary history coupled with low extinction rates. Inherent in this notion is the idea that speciation is an autonomous process. Quite opposite views have also been put

forward: species richness in the tropical rainforest is the consequence of a dramatically
fluctuating climate in the Pleistocene. There is no evidence at all in support of the basic
assumption that tropical and temperate biota differ in either of these respects. Explanations
for differences in species richness should be sought in present ecological factors.

Some recent analyses of diversity in different habitats (Currie and Paquin, 1987; Gentry
and Dodson, 1987) clearly show that species richness is strongly correlated with readily
measurable environmental parameters such as solar energy, mean annual temperature,
average annual precipitation, seasonality, elevation, and nutrient availability. It seems that
solar energy, seasonality, and elevation are the most important. Possibly, the total amount
of available energy is the most important factor, while other factors limit the possibility
of utilizing this resource. I fully agree with Moore (1987) that "forest richness, it seems,
is mainly the product of the resource base—water, warmth and solar energy."

The EcSC provides the conceptual coupling between taxonomy and ecology that makes
these views meaningful and approachable. If Moore's (1987) opinion is correct, then the
useful questions are: why does it pay to specialize, and how much? The question about
diversity is a matter, basically, of a cost-benefit analysis, like so many other fundamental
biological problems.

Literature Cited

Andersson, L. 1986. Revision of *Maranta* subgen. *Maranta* (Marantaceae). *Nord. J. Bot.* 6: 729–
    756.
Balslev, H., J. L. Luteyn, B. Øllgaard and L. B. Holm-Nielsen. 1987. Composition and structure of
    adjacent unflooded and floodplain forest in Amazonian Ecuador. *Opera Bot.* 92: 37–57.
Berry, P. E. 1982. The systematics and evolution of *Fuchsia* sect. *Fuchsia* (Onagraceae). *Ann. Missouri
    Bot. Gard.* 69: 1–198.
Burger, W. C. 1974. Ecological differentiation in some congeneric species of Costa Rican flowering
    plants. *Ann. Missouri Bot. Gard.* 61: 297–306.
Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
Cronquist, A. 1978. Once again, what is a species?. *Beltsville Symposia in Agricultural Research. 2.
    Biosystematics in Agriculture.*
———. 1988. *The Evolution and Classification of Flowering Plants,* ed. 2. New York Botanical
    Garden, New York.
Currie, D. J. and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees.
    Nature 329: 326–327.
Davis, P. H. and V. H. Heywood. 1963. *Principles of Angiosperm Taxonomy.* Oliver & Boyd,
    Edinburgh and London.
DuRietz, G. E. 1930. The fundamental units of biological taxonomy. *Svensk Bot. Tidskr.* 24: 333–
    428.
Gentry, A. H. 1988. Changes in plant community diversity and floristic composition on environ-
    mental and geographical gradients. *Ann. Missouri Bot. Gard.* 75: 1–34.
——— and C. Dodson. 1987. Contribution of nontrees to species richness of a tropical rain forest.
    Biotropica 19: 149–156.
Grant, V. 1981. *Plant Speciation,* ed. 2. Columbia Univ. Press, New York.
Hedberg, O. 1958. The taxonomic treatment of vicarious taxa. *Uppsala Univ. Årsskr.* 6: 186–195.
Hengeveld, R. 1988. Mayr's ecological species criterion. *Syst. Zool.* 37: 47–55.
Hennig, W. 1966. *Phylogenetic Systematics.* Univ. Illinois Press, Urbana.
Jonsell, B. 1984. The biological species concept reexamined. *In:* V. F. Grant (ed.), *Plant Biosys-
    tematics.* Academic Press, London.
Jonsell, L. and B. Jonsell. 1984. *Taraxacum. In:* Th. O. B. N. Krook and S. Almquist, *Svensk Flora.*
    Esselte Studium, Uppsala.
Knaben, G. 1954. *Saxifraga osloensis* n. sp., a tetraploid species of the *Tridactylites* section. *Nytt
    Mag. Bot.* 3: 117–138.
Levin, D. A. 1979. The nature of plant species. *Science* 204: 381–384.
Lidén, M. and B. Oxelman. 1989. Species—Pattern or process? *Taxon* 38: 228–232.
Mayr, E. 1982. *The Growth of Biological Thought.* Harvard Press, Cambridge, Massachusetts.
———. 1988. The why and how of species. *Biology and Philosophy* 3: 431–441.

Moore, P. D. 1987. Biological diversity. What makes a forest rich? *Nature* 329: 292.

Raven, P. H. 1978. Future directions in plant population biology. *In:* O. Solbrig et al. (eds.), *Topics in Plant Population Biology*. Columbia Univ. Press, New York.

———. 1980. Hybridization and the nature of species in higher plants. *Can. Bot. Assoc. Bull.* 13, suppl. 1: 3–10.

Schumann, K. 1902. Marantaceae. *In:* A. Engler (ed.), *Das Pflanzenreich* IV: 48.

Silvertown, J. W. 1982. *Introduction to Plant Population Ecology*. Longman, London and New York.

——— and R. Law. 1987. Do plants need niches? Some recent developments in plant community ecology. *Tree* 2: 24–26.

Simpson, G. G. 1961. *Principles of Animal Taxonomy*. Columbia Univ. Press, New York.

Stace, C. A. (ed.). 1975. *Hybridization and the Flora of the British Isles*. Academic Press, London.

Tutin, T. G. 1957. A contribution to the experimental taxonomy of *Poa annua* L. *Watsonia* 4: 1–10.

Van Valen, L. 1976. Ecological species, multispecies, and oaks. *Taxon* 25: 233–239.

Widén, K.-G. 1971. The genus *Agrostis* L. in eastern Fennoscandia. Taxonomy and distribution. *Flora Fennica* 5: 1–209.

Wiley, E. O. 1978. The evolutionary species concept reconsidered. *Syst. Zool.* 27: 17–26.

———. 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. John Wiley & Sons, New York.