An ontogenetic-ecological conception of species: a new approach to an old idea

Introduction

The observation that different species of organisms have different forms and behaviours may seem obvious. But what exactly does this mean and what makes a particular organism the kind of organism that it is? For instance, what makes a fox a fox? What makes foxes develop the characteristics that they do? What makes fennec foxes have large ears, termites consume wood and build mounds, wildebeest migrate, legumes fix nitrogen, or some female insects choose to lay their eggs on the leaves of specific plants? Our immediate response may be to say that these traits appear to be reliably passed on from one generation to the next among organisms of the same species. Or we may just say that organisms produce offspring like themselves. When we do this we rely on the general rule that 'like produce like.' Foxes produce foxes and frogs produce frogs. Frogs do not come from foxes, nor foxes from frogs.

This view may provide an initial explanation but is much less well-equipped when it comes to explaining similarities among different species of organisms. We can look to Haeckel to see why.

In his extensive embryological studies Haeckel observed morphological similarities shared across species (Haeckel 1866). In the illustrations of his *Generelle Morphologie* he depicted the strikingly similar forms shared by the embryos of pigs, crocodiles, mice, turtles, and platypuses at corresponding stages of development. Although somewhat exaggerated to support his ill-fated recapitulation theory, these illustrations emphasized a key feature of serial dimorphism. Embryos of different species were morphologically much more similar to each other than to the adult forms of their respective species.

Haeckel's observations of the similarities among different species introduced two concomitant problems: members of the same species may vary greatly in their morphological features, and organisms of the same species may display different morphological features at different stages in their life cycle.

The first of these problems is widespread among sexually reproducing organisms. The dimorphism between female and male mammals (e.g. tigresses and tigers), birds (e.g. mallard ducks and drakes), fish, barnacles, and arthropods means that the females of many species share a number of striking characteristics with females of different species (e.g. among the females of different species of mammals) that they do not share with the males of their own species.

In addition to sexual dimorphism, organisms of the same species may also display noticeably different morphological features at different stages in their life cycle. Consider the larval stage—the fleshy, leaf-eating, crawling, multi-pseudopod form of the worm-like caterpillar—of many species of butterflies and moths. The larval caterpillar of different species morphologically and behaviourally resemble each other much more than they resemble either the pupal, crysalis, or adult stage, in which they possess a thin body, six-legs, a long proboscis enabling them to extract nectar, large wings, the ability to fly, and (if female) lay eggs. This kind of sequential polyphenism is not exceptional. It occurs in most phyla where there are different developmental stages. As well as widely occurring in most animal phyla (e.g. in Chordata, Arthropoda, Porifera, Mollusca, and Cnidarians), it is arguably just as prevalent in many plant and fungi divisions (e.g. Angiospermae Rhodophyta, Ascomycota) (cf. Bishop et al 2006).

Serial changes over the life cycle are not limited to morphology and behaviour. These changes are often linked with associated ecological changes. Differences that occur within an organism's life cycle may include changes in diet (e.g. tadpoles of spadefoot toads may be omnivorous and then switch to being carnivorous as adults or vice versa depending on the availability of different food sources), alternate their leaf forms, seeds, and flower colour (e.g. heterophyllous aquatic plants produce different morphologies depending on whether they are growing in an aerial or underwater environment), or behavioural changes that correspond to changing ecologies (e.g. various stages of parasitic nematodes, such as *Pseudoterranova decipiens*, begin with a free swimming larvae, attachment to tissues in the peritoneal cavity of a crustacean host, migration to the muscle tissues, which, when ingested by a predator marine mammal develops into the adult form of the nematode and produces eggs) (cf. Anderson 1996: 1-5).

Because organisms show exceptional morphological, behavioural, and ecological transformations at different life stages, it makes them particularly unwieldy biological kinds to be conceived of in terms of the rule 'like produce like.' Adults of metamorphic species certainly do not produce larvae that are like themselves in terms of their morphology, physiology and behaviour. Adults may have been larvae at one time but the current form and behaviour of the adult cannot be said to be like that of its larvae.

Because of the morphological and behavioural differences between juveniles and adults of the same species at different life stages, some have suggested we should classify these as different species (cf. van Emden 1957).

Whilst recognizing the diversity among phenotypic features over an individual organism's life cycle, this suggestion must be rejected. Classifying juveniles and adults differently would pose a new set of metaphysical difficulties. A minimal requirement of any conception of species must be to treat an organism as a living being that may change over time but is (in some sense at least) the same individual throughout its life cycle.

In addition to the examples cited above, morphological and behavioural changes associated with growth and development are present in most species, albeit less prominent and more gradual than those of metamorphic species (cf. Werner and Gilliam 1984). If we do not accept van Emden's suggestion, our problem remains unresolved: If change over the life cycle is common to many if not most species, then what (if anything) is shared by organisms whose characteristics vary dramatically between different individuals purported to be from the same species?

There are innumerable ways in which organisms can be described and compared as similar to one another. But only a few of these provide generalizations that facilitate the making of hypotheses, directing experiments, and providing knowledge about species.

1.0 Species concepts and the species problem

To adequately explain how different forms and behaviours are maintained from parent to offspring within a species, what physical and behavioural characteristics or ancestral and ecological relationships determine species membership, and how species can be distinguished from one another, a specific conceptions of species is needed.

How to formulate a suitable conception of species to meet these diverse descriptive and explanatory needs makes up a large part of the ongoing discourse that has come to be known as the *species problem* (cf. edited collections by Mayr 1957, Ereshefsky 1992, Claridge, Dawah, Wilson 1997, Wilson 1999).

Of the variety of species concepts, the most influential as well as widely criticized has been Mayr's Biological Species Concept (BSC),(Mayr 1942, 1968). In the original form, the BSC stated that: "species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups" (Mayr 1942: 120). This conception of species answered the question, What makes an organism a member of a species?, in terms of an actual or potential physical connection (i.e. in terms of both the copulation of sexually mature organisms and in the generation of new organisms that result). This physical connection between members of the same species was thought to support the belief that there is indeed a natural division in biology upon which a natural classification can be based.

After discussing Mayr's revised BSC, I show how his and other gene-centred views of species share a bias for focusing exclusively on the adult stage of organisms. As an alternative, I'll then introduce what I call an ontogenetic-ecological conception of species. Although I criticize the BSC in particular, my own suggestion is not intended as a replacement. Instead it is intended as an additional conceptual tool of the species pluralist.

1.1 Mayr's updated BSC

In the middle of the 20th century a new, gene-centred understanding of natural selection, evolution, heredity, and the stability and variation within species became widely accepted (Mayr 1942, 1963, 1970, Dawkins 1976). This diverged from Darwin's original conception of descent with modification by taking genes as the causally most important factors in evolution and in the development of organismal form. In *The Selfish Gene*, Dawkins described how genes, not organisms, were the "motors of evolution." Genes build organisms that are vehicles for their own replication. This view was later extended to include all morphological traits, behaviours, social relationships, and habitats of organisms; they are merely "phenotypic effects of a gene … [they] are the tools by which it levers itself into the next generation, and these tools may 'extend' far outside the body in which the gene sits, even reaching deep into the nervous systems of other organisms" (Dawkins 1982: vi).

In an attempt to accommodate these extended environmental features, a revised genes-plus-environment view of Mayr's BSC resulted:

> This concept stresses the fact that species consist of populations and that species have reality and an internal genetic cohesion owing to the historically evolved genetic program that is shared by all members of the species. According to this concept, then, the members of a species constitute (1) a reproductive community. The individuals of a species of animals respond to one another as potential mates and seek one another for the purpose of reproduction. The species is also (2) an ecological unit that, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment. The species, finally, is (3) a genetic unit consisting of a large intercommunicating gene pool, whereas an individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time (Mayr 1992: 17).

This new account of species took biological form to be the result of two ontologically separate but interacting spheres of activity: moulding by a naturally selecting environment and the unfolding of the information contained within an organism’s genetic program. The selecting environment gradually modifies generations of organism’s phenotypic traits on the basis of whether they increase or decrease the likelihood of the organism to successfully mate and pass on its genes to future offspring. Those genes that are reliably passed down from parent to offspring contribute to the species-specific blueprint for building new organisms of the next generation of the species. The species gene pool is the result of the selecting force of the environment on genetic mutations occurring over numerous generations.

The organizational form of organisms is in a sense pre-formed—written in its genetic code. The organism’s internal genetic code interacts with the external environment through the course of its ontogeny. Organismal ontogeny amounts to translating the information in the genetic code into a design blueprint that can be used to build an adult organism.

Although this perspective conceives organismal organization as the result of both genes and the environment, these are not treated as equal interactants. Genetic causes are systematically privileged as the primary source of causal power, whereas extragenetic causes or environmental causes are considered secondary or as contributory to these. They are bracketed off as background conditions within which genes operate. This results in the genes, rather than every other causal factor, being most important (Griffiths and Gray 2001: 195, Laland, Odling-Smee, and Feldman 2001: 120). Mayr emphasizes this causal disparity: "the basic biological meaning of the species is a protected gene pool” (Mayr 1992: 17).

This updated BSC systematically privileges the inherited genes as the true cause of species specificity. They provide the "internal genetic cohesion [and] genetic program that is shared by all members of the species” (Mayr 1992: 17). For Mayr, what makes a species real is this genetic cohesion: "species have reality and an internal genetic cohesion owing to the historically evolved genetic program that is shared by all members of the species” (Mayr 1992: 17). Consequences of these commitments will be explored with regard to the assumption that species are cohesive entities over the next few sections.

2.0 The BSC's heavy reliance on species' "genetic cohesion"

The shared species-specific genetic program is both the cause of a species' cohesion and gives a species its metaphysical reality. The genetic cohesion of a species is maintained through actual or potential gene flow between its members; this provides a physical connectedness of individual organisms to other conspecifics. Mayr emphasizes the importance of this exchange of genes because he believes "mixing the genes of two different species leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection" (Mayr 1992).[1] As such, species are properly understood as protected gene pools. The protection of a species' gene pool is ensured by what Mayr calls "cohesive mechanisms" that "protect it from harmful gene flow from other gene pools" (Mayr 1992: 17). Organisms that share the same gene pool are thought to have access to any genetic mutations which may arise in individuals throughout the species population. Because genotypes are causally determinative of phenotypes, if the gene pool is shared so is the phenotypic expression of these genes. If the phenotypic expressions of the organisms were relatively homogeneous, then natural selection would act uniformly in the population. This would ultimately mean that natural selection would restrict the possibility of persistent and stable polymorphisms among subgroups which could eventually lead to speciation.

Reliance on the restriction of gene flow between members of different species is based on an assumption that unrestricted gene flow between members of different species cannot be sustained. If there is unrestricted gene flow between members of different species, the current diversity of species would cease to exist. Such unrestricted gene flow would result in the two species becoming less genotypically and phenotypically distinct. Increased gene flow between individuals of different species would eventually result in the two previously separate species merging to form one genetically and phenotypically amorphous species (Mayr 1970). If reproductive relationships and gene flow were not restricted to conspecifics, an increasingly homogeneous gene pool shared by organisms of different species would result. By producing an increasing homogeneity of both genotypes and phenotypes of organisms as the boundaries between species eroded, Mayr worries this would result in a decrease in the biodiversity (Mayr 1982).

---

[1] The opposite has been observed with regard to bacterial species. In some, it is in the combining and exchanging of genetic materials with heterospecifics that allow individuals of a particular species to acquire resources enabling them to construct evolutionarily advantageous phenotypes.

In contrast, new species are formed when populations become reproductively isolated from one another and gene flow between these groups stops. Species are separated from one another "by a complete biological discontinuity" (Mayr 1992: 20). It is this complete separation from other species which "protects [the species] from harmful gene flow from other gene pools" (Mayr 1992: 17). Different species are sharply demarcated from one another by what Mayr calls a "gap." This gap "exists between populations that coexist … at a single locality at a given time which delimits the species … one finds each species clearly delimited and sharply separated from all other species" (Mayr 1992: 19). He highlights the crucial significance of this sharp discontinuity between species: "Most important, no hybrids or intermediates [are] among these [different] species … each is a separate genetic … system separated from the others by a complete biological discontinuity, a gap" (Mayr 1992: 20).

Mayr understands species cohesion in terms of gene flow, genetic homeostasis, and common selective pressure. Viewing species as genetically cohesive units is not unique to the BSC. A number of other conceptions of species including the isolation, cohesion, mate recognition, reproductive, phylogenetic, cladist, and evolutionary conceptions of species share this view (Ereshefsky 1992: 385-87). The BSC, isolation, reproductive, and mate recognition conceptions of species explicitly rely on the importance of potential or actual physical relationships of sexual reproduction and the exchange of genes between conspecifics it facilitates as justification for internal species genetic cohesion and genetic isolation from members of other species.

Cladistic and phylogenetic species concepts (PSC) implicitly rely on reproductive relationships and genetic cohesion for the neatly bifurcating pattern of unbroken and unreticulated lineages central to both. Genetic cohesion and genetic isolation are assumed by these species concepts in their definition of species as an unbroken lineage—a lineage maintained by a sequence of reproductive relationships restricted to conspecifics and ensured by exclusive vertical transmission of genetic material from one generation to the next. The PSC conceives of species in terms of the bifurcating branching tree pattern of evolution. It identifies species in terms of a group of organisms which share a monophyletic lineage (McKitrick and Zink 1988). A monophyletic lineage is an unbroken sequence of ancestor-descendents that includes all and only the descendents of one common ancestor. The PSC denies specieshood to any groups of organisms that are the descendents of more than one common ancestor. By ruling out paraphyletic lineages, it denies specieshood to groups of organisms which includes some but not all of the descendants of a common ancestor.

Although intended to explain the unifying features of a species (as well as those separating species from each other), talk of species cohesiveness, cohesive mechanisms, and genetic cohesion does not succeed in explaining this unity of (or the disunity between) species but succeeds only in presupposing it (cf. Ereshefsky 1992: 381-87). Although problematic, the assumptions of species cohesion and the apparent circular arguments on which they are based are widely held.

3.0 The adult-centred bias of many species concepts

Species concepts such as the BSC, phylogenetic, mate recognition, cladist, isolation, cohesion and genetic rely on the adult form as central to understanding and articulating the characteristics and behaviours of a species. For example, Mayr's BSC holds that a species is an isolated reproductive community that shares a gene pool. The community is made up of organisms that can actually or potentially interbreed with one another (cf. Mayr 1957, 1992). As has been discussed above, the inheritance of genes and shared gene pools play a central role in many conceptions of species. If genetic cohesion and shared gene pools define a species, then it follows that the individuals to focus on are reproductively mature adults. Species are thought to be best understood in term of the morphologies and behaviours of adults because they are the vehicles within which lie the potential for genetic cohesion.

The selection of sexually mature adults over other stages of the life cycle rests on the underlying assumption that all species can be characterized as a cohesive biological kind where cohesion is understood to be fully explained in terms of actual or potential sexual reproductive relationships, shared gene pool, barriers to sexual reproduction with members of other species, recognition of conspecific mates. This may be a necessary but it is not a sufficient condition of specieshood for sexually reproducing animals. This way of characterizing species does not apply to numerous hybridizing plant species and bacterial species. These are better understood in terms of ecological or polyphasic species concepts, respectively (van Valen 1976, Vandamme et al. 1996) or in some cases phenetic concepts.

Systematic and exclusive focus on the adult form for classifying species rests on an underlying assumption that organisms only fully manifest their true species nature in adulthood. It overemphasizes the role of reproduction and ancestry in ensuring similarity across generations and in doing so ignores the diversity of ontogeny. Disregarding these developmental changes to the organism over its lifetime denies the role these continual changes play in defining the characteristic morphologies and behaviours of the species (not just in the adult stage but in all stages of the life cycle). In focusing exclusively on the adult organism and reproductive relationships between sexually mature individuals, many conceptions of species effectively ignore the rest of the life cycle.

4.0 Buffon's suggestion

Although the discussion of species concepts and the species problem are usually conceived of in terms of contemporary debates over whether phylogenetic, polyphasic, ecological or cladist conceptions best answer the question "what is a species?" These discussions have deep historical roots. One of the earliest and unfortunately somewhat overlooked suggestions is that given by the French naturalist Buffon (but see Gayon 1996). Buffon's suggestion for a new conception for species has two parts: 1) an outline for an comprehensive understanding of species that included morphological, physiological, and behavioural characteristics of the different ontogenetic stages of the life cycle as well as the different ecological niches inhabited within each stage, and 2) a practical guide for critically observing, recording, and organizing the particularities of organisms (Buffon 1749).

Producing an extensive catalogue of his own meticulous observations and descriptions, Buffon argued that it was only after studying the minutiae of an organism's organization and behaviour that it is possible to organize these facts to make generalizations about organisms of a particular species as well as comparisons both within the species and between different species (Buffon 1949:97-104). Our knowledge of species is acquired through the precise description of an organism's morphology, internal activities (digestion), external activities (locomotion), and its mode of living within its environment—not from ideal abstract knowledge of essences or universal truths (Buffon 1749: 100-11).

His view of species was revolutionary. Buffon was the first to include a full description of species within his formal view. This included the ecological, ontogenetic, and stage-specific behaviours of species as well as their form, size, mode of motility, position of rest, location of organs, their functions, and the history of the individual organism:

> [organisms'] conception, the time of gestation, [the] birth, the number of young, the care shown by the parents, their sort of education, their instinct, the places where they live, their

> nourishment and their manner of procuring it, their customs… their hunting, and finally, the services which they can render to us and all the uses which we can make of them (Buffon 1749: 111).

This admittedly cumbersome description of every organism was not intended to be complete, but was to be constantly amended with new observations and findings (Buffon 1749: 113).

4.1 An ontogenetic-ecological conception of species

I suggest that revision to Buffon's conception of species may provide the basis for a conception of species that includes the whole, temporally extended and ecologically embedded, life cycle of organisms. This is admittedly a much different view than that proposed by the BSC. It's aim is much broader but it does not conflict with Mayr's view. The BSC can be understood as a limited case of the view proposed in this paper. Mayr's reliance on gene flow as facilitated by reproductive relationships of conspecifics meant that the focus of the BSC is on one stage of an organism's life cycle—sexual maturity. The focus on sexually mature adult organisms is justified by the view.

The ontogenetic-ecological conception of species takes ontogeny and ecology of an species to be as important as its phylogeny. Each developmental stage of an organism's life cycle has its own ontogeny. The phylogeny of a species is then simply the history of a specific series of contingent self-constructed individual life cycles. When we consider the adult stage of the organism's development we can't but help to also focus on the stages that came before. The adult stage cannot be understood in isolation. Its embryological form, juvenile structures and development, and the learned behaviours and interactions of earlier stages all contribute to the phenotypes and behaviours are retained within its adult stage. The adult stage is contingent on what came before. Like any other developmental stage, the adult stage is just a "temporal slice through the life cycle. It carries the evidence of past gene transcriptions, mechanical influences inside and outside the organism, results of past activities, nutrition or lack of it, and so on" (Oyama 2000: 161).

At different stages in the life cycle, various organisms may display different morphologies or behaviours associated with a particular stage or in a specific environment. Among most organisms ontogeny involves constant changes. On the adult-centred view of species, development over an organism's life cycle is understood as the processes necessary in building an adult. Species are conceived in terms of the final output of this process—the adult organism. The life cycle of an organism is treated as the means necessary for building an adult which is then the object of species classification and study. In contrast, the whole life cycle view suggested here conceives species in terms of a sequence of constructed and reconstructed self-organizing activities of organisms over their life cycles which include the morphological and behavioural characteristics in each stage—not just that of the adult.

I suggest that much of the problem with competing species concepts is that they rely almost exclusively on the characteristics and behaviours of sexually mature adults to explain all characteristics of the entire species. This is no doubt an effective way to find phylogenetic groups. However, what is left out—the ontogeny of the species life cycle is crucial to understanding both how the species lives, changes according to its environment. To flesh out the genetic phylogeny of species we need also to look at the ecologically embedded ontogeny of them.

In fixing on the reproductive capacities of adult organisms, many species concepts ignore the role of learnt behaviours, inherited niches, modes of living, environmental and ecological changes, as well as the organism's non-sexual interaction with both con- and hetero-specifics throughout each of the stages of its life cycle.

The proposed conception of species outlined in this paper aims to provide an alternative perspective on species and in doing so avoiding some of the underlying assumptions held by the BSC and other gene-centred species concepts. It began with a characterisation of the species problem and some of the assumptions underpinning some of the conceptions of species. It then revealed an underlying bias of these conceptions to focus exclusively on the adult stage of the life cycle in articulating what a species is. It was then shown that this bias has led not only to the omission of behavioural and morphological differences crucial to understanding species, but also to the changes in ecological niches associated with each life stage. Lastly, it offered a broader conception for species that included not just the behaviours and morphologies of the adult stage but also the ecological differences associated with each stage of the life cycle. This conception of species is not suggested in opposition to the adult-centred species concepts as it is consistent with most. Its role is to augment these, offering an additional conceptual tool to the species pluralist.

Bibliography

Anderson, R. (1996) Why do fish have so few roundworm (nematode) parasites? Environmental Biology of Fishes 46: 1-5.

Bishop, C., Erezyilmaz, D., Flatt, T., Georgious, D., Hadfield, M., Heyland, A., Hodin, J., Jacobs. M., Maslakova, S., Pires, S., Reitzel, A., Santagata, S., Tanaka, K. and J. Youson (2006) What is metamorphosis? Integrative and Comparative Biology 46(6):655-661.

Buffon, G-L. comte de (1749/1981) Historie naturelle, générale et particulière avec la description du cabinet du Roi. Sanson. Deux-Ponts. [pirated edition] and J. Piveteau. [Paris edition]. Reprinted in From Natural History to the History of Nature: Readings from Buffon and his critics, J. Lyon and P. Sloan (trans). University of Notre Dame Press, Notre Dame.

Claridge, M. F., Dawah, H. A. and Wilson, M. R. (eds.) (1997) *Species: the Units of Biodiversity*. Chapman and Hall, London.

Dawkins, R. (1976/1989) The Selfish Gene. Oxford University Press. 2nd edition, Oxford.

—— (1982) The Extended Phenotype. Freeman, Oxford.

Emden, F. van, (1957) The taxonomic significance of the characters of immature insects. *Annual Review of Entomology* 2: 91-106.

Ereshefsky, M. (1992) The Units of Evolution: Essays on the Nature of Species. MIT Press, Cambridge.

Ereshefsky, M. (1992) Species, Higher taxa, and the units of evolution. In M. Ereshefsky (ed.), The Units of Evolution. MIT Press, Cambridge.

Griffiths, P. and Gray, R. (2001) Darwinism and developmental systems. In S. Oyama, P. Griffiths and R. Gray (eds.), Cycles of Contingency. MIT Press, Cambridge.

Gayon, J. (1996) The individuality of the species: a Darwinian Theory?—From Buffon to Ghiselin, and Back to Darwin. Biology and Philosophy 11: 215-244.

Haeckel, E. (1866) Generelle Morphologie der Organismen. Reimer, Berlin.

Laland, K., Odling-Smee, F., and Feldman, M. (2001) Niche construction, ecological inheritance, and cycles of contingency in evolution. In S. Oyama, P. Griffiths and R. Gray (eds.), Cycles of Contingency. MIT Press, Cambridge.

Mayr, E. (1942) Systematics and the Origin of Species from the Viewpoint of a Zoologist. Columbia University Press, New York.

—— (ed.)(1957) *The Species Problem*. Amer. Assoc. Adv.Sci., Publication no. 50.

—— (1963) Animal Species and Evolution. Harvard University Press, Cambridge

—— (1968) Comments on theories and hypotheses in biology. Boston Studies in the Philosophy of Science. 5. Reprinted in Mayr, E. (1976) Evolution and the Diversity of Life. Belknap Press of Harvard, Cambridge.

—— (1970) Populations, Species and Evolution. Belknap Press of Harvard, Cambridge.

—— (1992) Species concepts and their application. In M. Ereshefsky (ed.), The Units of Evolution. MIT Press, Cambridge.

McKitrick, M. C. and Zink R. M. (1988) Species concepts in ornithology. Condor 90: 1-14.

Oyama, S. (2000) The Ontogeny of Information. 2nd edition. Duke University Press, Durham.

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

Vandamme, P., Pot, B., Gillis, M., De Vos, P., Kersters, K., and Swings, J. (1996) Polyphasic Taxonomy, a consensus approach to bacterial systematics. Microbiological Reviews 60 (2): 407-438.

Van Valen, L. (1976) Ecological species, multispecies, and oaks. *Taxon*. 25(2/3): 233-239

Werner, E. and Gilliam, J. (1984) The ontogenetic niches and species interations in size-structured populations. Ann Rev. Ecol Syst. 15: 393-425.

Wilson, R. (ed.) (1999) *Species: New Interdisciplinary Essays*, MIT Press, Cambridge.