CORRESPONDENCE

Species and speciation

In his stimulating TREE review on sympatric speciation, Guy Bush stated that "Trying to explain speciation within the context of a preconceived species concept places the cart before the horse!" He continued: "Speciation does not depend on the a priori invocation of any particular species definition. These are truly remarkable statements and are tantamount to suggesting that we must understand processes before we can observe and describe the natural phenomena that they produce. It certainly seems to me that Bush has confused the cart with the horse.

In the body of his review, Bush I clearly does not follow his own prescription. It is quite obvious that he is using a biological species concept when he writes of the 'evolution of reproductive isolation' and the need to 'identify key traits responsible for mate recognition'. Only if some variant of the biological species concept is used may speciation be regarded as the evolution of reproductive isolation2,4. According that, then I agree with Bush that most critical to understanding speciation processes is determining whether an initial reduction in gene flow between incipient species populations results from either extrinsic, geographical (or spatial) barriers on the one hand, or intrinsic, genetic barriers within a population on the other. This is the essential difference between theories of allopatric and sympatric speciations.

This conception of species definitions is not simply a semantic one, since other now commonly advocated species concepts have different repercussions for speciation theory. For example, variants of a phylogenetic concept are widely advocated by systematists primarily concerned with cladistic analyses5,6. Typical are Nixon and Wheeler7, who define species as '...the smallest aggregate of populations or lineages diagnosable by a unique combination of character states...'. No reference is made here to reproductive isolation or specific mate recognition. Clearly, it is very important that a wide debate should now be held on the nature of species - generally recognized as the units of biodiversity. The nature of speciation processes can only be investigated and understood when there is agreement on the nature of species.

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References

Reply from G.L. Bush

We have shown theoretically that speciation, when defined as the differentiation of taxa into lineages irreversibly committed to distinct evolutionary fates, can occur in the presence of gene flow. This speciation process is particularly important in groups such as birds and mammals in which most taxa are narrow specialists (habitat and host) and often sympatric. Unfortunately, we cannot define the exact moment when the lineages are irreversibly split; thus, precise definition of what a species is in these cases is not yet possible.

The biological species concept (BSC) can only be applied legitimately to sympatric taxa. If there is evidence of gene flow, interbreeding taxa are regarded as members of a polymorphic species. Indeed, some advocates of the BSC maintain that races can only evolve and exist allopatrically as they would fuse into one interbreeding population if sympatric. Strict adherence to the BSC thus precludes sympatric race formation and speciation, which clearly occur in nature. Speciation (the splitting of lineages), may occur long before complete reproductive isolation evolves. Reproductive isolation is only the end product of the speciation process, not its cause, and it is in this context that I use the term. Two diverging sister taxa may interbreed and exchange some genetic information, yet maintain their phenotypic identity. Such taxa behavior can be recognized as 'good species'. Are we to disregard these taxa as units of biodiversity because they do not meet the criteria of complete reproductive isolation prescribed by the BSC?

Strict adherence to any one particular species concept may actually impede our understanding of the speciation process. In addition, putting such limitations on our conceptual framework may very well eliminate many biologically unique and important taxa from consideration in the effort to preserve biodiversity.

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References

Scientific research traditions and collaboration in tropical ecology

In his recent TREE postscript, Shine2 remarks that biologically impoverished, financially wealthy nations with long academic histories and predictable climates (such as Sweden) foster ecological research that is conceptual, theoretical and experimental. In tropical nations, with vastly greater biological diversity and biological systems that are shaped by episodic events, we find more routine, descriptive, survey-driven research. This is not surprising. Many tropical countries are financially strapped and may not have the will, the time or the centuries-old tradition of academic enquiry that foster conceptual experimental research. Increased collaboration between ecologists in temperate and tropical institutions is an effective way to address biodiversity conservation problems, broaden ecological theory to account for non-equilibrium ecosystems1, and simply counter the negative correlation between the density of ecologists and the diversity of species. But for fruitful collaboration, improved attitudes on the part of host governments, funding agencies, and sometimes researchers themselves, are necessary.

In countries such as Namibia, we have an enormous task just doing descriptive research of the sort wrapped up in Europe a century ago. Ecologists with the inclination to pursue current hypotheses, or delve deeper into their systems, usually have to do it withers. We have a huge array of little-known species, but few skilled taxonomists and ecologists, dwindling or nonexistent budgets, haphazard museum collections8, and governments and university researchers who focus on what is commercially important in and host to basic scientific research. Even ecological and taxonomic studies essential for conservation work are un or undersupported. University biology departments that should lead such research are often pressed into animal husbandry or crop development - when, indeed, they have time and funds for research at all. With such appalling constraints, it is hardly surprising that few tropical ecologists contribute to the development of ecological theory. So the most diverse, most vulnerable and potentially most scientifically rewarding systems often occur in the countries least equipped to study them. This irony is well known but not amusntable. We need increased links between well-funded institutions in depauperate nations and ill-funded ones in speciosc nations. And we in the tropics need to appreciate the interdependence of descriptive and productive ecology. There is a widespread perception among southern ecologists that hypothesis-testing is a bourgeois pastime, that 'pure' research is irrelevant, and that students need not understand the scientific method. Yet ecological description alone amounts to little more than a hill of beans. A more comprehensive body of theory, developed from our own ecosystems and study species, would help us to predict more accurately how species respond to disturbance or harvesting, whether they can recognize areas of local extinction, or whether small isolated populations will survive. That is not a luxury; indeed it is an urgently needed timesaving measure. It allows us to generalize more confidently from those species and systems we understand to those we don't. We also need a better appreciation of interdisciplinary approaches. For example, behavioural ecology (regarded initially by some of my colleagues in Namibia as a particularly tenuous indulgence) is a critical ingredient, with conservation genetics and biogeography, for determining effective population sizes of managed species? These needs are effectively met through collaboration with northern

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