a multistage process. If pre- and post-isolating mechanisms are part-and-parcel of an inevitable evolutionary drive towards taxonomic diversification, then they should be treated as such in all their fascination, and not as part of an inclusive defining moment.

So, where do we go from here? After all, we all know and love species. They are the units of functional cohesion of populations of similar individuals that are the focus of our research programmes. The path to take, according to Mallet, is to provide, as a minimalist objective, a definition that does not confuse process with pattern. For this he proposes the 'genotypic cluster definition', meaning that collections of genetic and phenotypic markers that are collectively shared by a group of individuals, and which are not shared with other groups (recognized through their own shared clusters), would constitute a species.

I have two problems with this: one trivial and one non-trivial. First, Mallet wishes to discriminate between the 'genotypic cluster definition' and the 'phylogenetic species concept' of Cracraft, which is based on the supposed species-uniqueness of apomorphies. As Mallet points out, the resolving power of modern molecular techniques is capable of providing individual-specific apomorphies, so getting us nowhere. Clusters of apomorphies shared by individuals (essentially the genotypic cluster definition) might seem to get around this problem but it still doesn't provide a workable guide as to how we isolate a species from the lower and higher taxonomic units. And indeed, why should we bother if, as Darwin argues, species are a transition stage in a much grander process of incessant bifurcation.

More importantly, the genotypic cluster definition suffers, as almost all previous species definitions, for representing organisms as unusually static objects. This is unfortunate, for it ignores one of the most fundamental aspects of all eukaryotic species with alternating haploid–diploid phases: that at each new generation two haploid sets of genetic instructions coexist in the same nucleus and that, if the instructions are not compatible one with another, then the diploid phase suffers. What then distinguishes individuals belonging to one eukaryotic species from those belonging to another is that there is sufficient similarity between their genomes to ensure a safe passage from one generation to another and through diploid-phase ontogeny. On this basis, the genotypic/phenotypic markers of the cluster definition are just the tip of the iceberg of the all important species-specific genetic programmes that govern diploid, multicellular development.

It is, then, within this perspective that sex (random chromosome assortment coupled to random gamete fusion) reaches its true significance as a process that ensures that haploid genomes remain genetically similar and functionally compatible. At the heart of sex is meiosis, which also provides the opportunity for a variety of genetic homogenizing systems to occur[2]. On this basis, the ultimate effect of sex and meiosis should be regarded as more a means for the prevention of genetic differentiation of haploid genomes (as occurs in bacteria and clonal asexual eukaryotes) rather than solely as a provider of genetic variation. It does, indeed, provide inter-individual variation but not to the extent that recombinant chromosomes disrupt the essential functional compatibility between newly associated haploid sets in the developing diploid phase. There is a clear link here with Templeton's emphasis on 'cohesion mechanisms' that underpin the species concept[3].

If we take this functional approach to the integrated distinctiveness of sexual species seriously then one of the key unanswered questions in evolutionary biology is why should happily coexisting sets of chromosomes, forever shuffled into new average combinations and enjoying the genetic 'cross-talk' of meiosis, split into two functionally incompatible sets of chromosomes and genetic instructions?

It is inevitable that all three major processes of population differentiation (natural selection, neutral drift and molecular drive) are involved in this question, in complex and intriguing ways. From recent studies in some cellular and developmental operations, it is becoming clear that many species share very similar key biological functions but that the precise molecular manner in which such functions are brought into effect differ between species. In other words, while molecules A and B in one species and A^1 and B^1 in another are compatible with each other, interspecific mixtures of A and B^1 and A^1 and B are not compatible. Hence, A and B have the essential capacity to coevolve (often the result of an interaction between natural selection and molecular drive[4,5]). By such means, key biological functions are maintained while species differentiation proceeds. Molecular coevolution and its emphasis on the functional interactive biology of genes is but one example of the types of phenomena we should be exploring if we are to understand the dynamics of speciation. A major headache ahead of us but ultimately tractable. From such studies, a functional species definition will emerge by rights.

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References

1 Mallet, J. (1995) *Trends Ecol. Evol.* 10, 294–299
2 Dover, G.A. (1982) *Nature* 299, 111–117
3 Templeton, A.R. (1989) in *Speciation and its Consequences* (Otte, D. and Endler, J.A., eds), pp. 3–27, Sinauer
4 Dover, G.A. and Flavell, R.B. (1984) *Cell* 38, 623–624
5 Dover, G.A. (1992) *BioEssays* 14, 281–287

Mallet[1] recently transcribed the so-called biological species concept (BSC) in a logically superior way under the heading 'genotypic cluster definition' (without providing a definition as such). He pointed out that the BSC is not a product of the Modern Synthesis but much older. I cannot agree more, and would like to add that mid-19th-century practising malacologists even preceded the authors cited by Mallet. For example, the evolutionist Mousson[2] wrote (in German): 'The species is the total of individuals, interconnected by descent and reproduction, maintaining unlimited reproductive capacities' (p. 13). He recognized polytypic species ('*Formenkreise*') and emphasized the difference between sympatric and allopatric occurrences; systematists should investigate 'whether or not the forms of *a single* area are interconnected by all possible intermediate forms and ways of life, and whether forms of *different* areas, followed topographically, gradually change into each other ...' (pp. 7–8).

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References

1 Mallet, J. (1995) *Trends Ecol. Evol.* 10, 294–299
2 Mousson, A. (1849) *Die Land- und Süsswasser-Mollusken von Java*, Friedrich Schultess, Zürich

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Reply from J. Mallet

Many 'good' species hybridize in nature – about 10% of animals such as birds and butterflies[1,2] and even more among plants[3]. Even the largest animal that has ever existed, the blue whale (*Balaenoptera musculus*) hybridizes successfully with the fin whale (*B. physalus*)[4]. A definition of species based on interbreeding, like the BSC, simply isn't practical. In addition, the BSC runs into theoretical difficulties when used in tests of hypotheses of speciation, because the assumption of species cohesion via gene flow makes speciation appear more difficult than necessary[5].

So the BSC and other assumption-laden definitions, such as the recognition, cohesion and phylogenetic concepts, are neither useful in practice nor in evolutionary theory. Instead, we must accept that species are man-made groupings whose importance to us is operational; species do not necessarily define themselves by means of an underlying biological 'essence'. The belief that definitions need to be based on 'concepts' rooted in the true 'essence' of the thing to be defined dates from Plato and Aristotle, and was revived by Hegel, who is much admired by Mayr[6]. The rest of modern science, meanwhile, now avoids essentialistic definitions[7]. For example, nobody argues about definitions of stars: a star is simply a very massive object that emits light. A number of evolutionary biologists have recently realized that species can be better defined by modifying Darwin's operational definition to include genetic evidence[5]. A suitable definition (supplied and demonstrated in my *TREE* article, despite Gittenberger's assertion to the contrary) is that species are groups that remain recognizable in sympatry because of the morphological and genotypic gaps between them. This kind of species is free to hybridize in theory as well as in practice; and can evolve via reticulation, as well as in the strictly hierarchical mode assumed under the phylogenetic concept. It is curious, therefore, that Gittenberger accuses me of having 'transcribed' the BSC. I feel that the BSC and all other essentialist definitions, should be scrapped once and for all; an operational or nominalistic definition is all we need. However, I agree with Gittenberger that precursors of the BSC have a long pre-darwinian history; this has also been well documented by Mayr[6].

Dover appears to agree with me that the BSC and derivatives cause circular thinking, but then argues that I should have considered species to be 'units of functional cohesion', rather than use an assumption-free definition. Dover exhumes a Dobzhansky/Mayr idea I would love to bury, that the 'function' of gene flow and sex within species is to 'integrate' or 'homogenize' genetic variation. If this means anything at all, it is suspect because it implies group selection on a species-wide scale. This loaded kind of definition is just what I was trying to avoid; it implies that speciation will be difficult since it must break down the postulated internal 'cohesion mechanisms', as Dover himself shows. On the other hand, arguments about species *concepts* such as this are interesting, mainly because they are really evolutionary arguments about how species can remain distinct from one another. But they will not result in better ways of defining species.

Dover thinks I follow Darwin in holding that there are no such things as species. Actually, I believe that Darwin's discussions of species have been misinterpreted, especially by Mayr[6], and that Darwin had a clear understanding of the gaps between species. Races, species and genera are the same *kinds* of things, but a sensible dividing line between species and races is the existence of separate genotypic clusters in sympatry[5]; any naturalist or taxonomist knows that gaps between such clusters do exist. This definition is conservative, being close to the level where most practising taxonomists place species. In fact, it is roughly at the level considered relevant by supporters of the BSC, while avoiding the BSC's theoretical overheads. Finally the genotypic cluster definition is at that level most interesting to evolutionists like myself who claim to study speciation.

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References

1 Grant, P.R. and Grant, B.R. (1992) *Science* 256, 193–197
2 Guillaumin, M. and Descimon, H. (1976) in *Les Problèmes de l'Espèce dans le Règne Animal, Vol. 1* (Bocquet, C., Génermont, J. and Lamotte, M., eds), pp. 129–201, Société Zoologique de France
3 Stace, C.A. (1991) *New Flora of the British Isles*, Cambridge University Press
4 Avise, J.C. (1994) *Molecular Markers, Natural History and Evolution*, Chapman & Hall
5 Mallet, J. (1995) *Trends Ecol. Evol.* 10, 294–299
6 Mayr, E. (1982) *The Growth of Biological Thought*, Belknap
7 Popper, K.R. (1966) *The Open Society and its Enemies* (5th edn), Princeton University Press

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Spatial dynamics and chaos

In their *TREE* review, Bascompte and Solé[1] examine the population dynamic consequences of explicitly incorporating the spatial dimension into ecological models. A major argument advanced is that 'complex motion is enhanced by dispersion' and to support this assertion, Bascompte and Solé refer to examples of diffusion-induced chaos[2,3]. It is well known that in continuous-time models, at least three variables are necessary for the emergence of chaotic oscillations; this requirement is relaxed with the inclusion of spatial degrees of freedom[4]. This destabilizing mechanism does not transfer to discrete-time models, however, where chaos can be observed in even the simplest one-dimensional models[5]. While there are some extreme cases of dispersal having a destabilizing influence[6,7], it has been shown that spatial coupling usually does not alter the stability properties of a discrete-time system[8–11]. This is in direct contrast to the claims of Bascompte and Solé who, based mostly on their own research[12,13], propose that equilibrium stability decreases as the spatial domain is increased – a phenomenon which they call a spatially induced bifurcation.

The findings of Bascompte and Solé's earlier work[12,13] arise solely as a result of biologically impossible assumptions embedded within their models[10,14]. Phrased as discrete analogues of reaction-diffusion equations, their models impose the processes of competition and dispersal on the same individuals. While in reaction–diffusion models (which concern infinitesimal rates of change) this assumption is valid, in discrete-time and discrete-space models, it can lead to the same individuals dying and yet dispersing; this mechanism is also responsible for the generation of negative population densities in their models. Bascompte and Solé have argued elsewhere[15] that their formalism is intended to reflect a scenario where individuals compete for resources and then disperse within the same life-stage. When an individual-based model is employed to explore this situation (thus avoiding the pitfall of generating negative densities), the stability boundaries of the model remain unaffected by dispersal[16].

In conclusion, while Bascompte and Solé's review is both interesting and very timely, some of the results they present are contradicted by other studies, and have been shown to depend critically on the specific (and controversial) fashion in which their models are formulated.

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References

1 Bascompte, J. and Solé, R.V. (1995) *Trends Ecol. Evol.* 10, 361–366
2 Kuramoto, Y. (1984) *Chemical Oscillations, Waves and Turbulence*, Springer-Verlag
3 Pascual, M. (1993) *Proc. R. Soc. London Ser. B* 251, 1–7
4 Kot, M. (1989) *Biosystems* 22, 279–287
5 May, R.M. (1976) *Nature* 261, 459–467
6 Reeve, J.D. (1988) *Am. Nat.* 132, 810–836
7 Hastings, A. (1992) *Theor. Popul. Biol.* 41, 388–400
8 Allen, J.C. (1975) *Am. Nat.* 109, 319–342
9 Gyllenberg, M., Söderbacka, G. and Ericsson, S. (1993) *Math. Biosci.* 118, 25–49
10 Hassell, M.P., Miramontes, O., Rohani, P. and May, R.M. (1995) *J. Anim. Ecol.* 64, 662–664
11 Rohani, P., May, R.M. and Hassell, M.P. *J. Theor. Biol.* (in press)
12 Solé, R.V. and Vallis, J. (1992) *J. Theor. Biol.* 155, 87–102
13 Bascompte, J. and Solé, R.V. (1994) *J. Anim. Ecol.* 63, 256–264
14 Stone, L. (1994) *Nature* 367, 418
15 Bascompte, J. and Solé, R.V. (1995) *J. Anim. Ecol.* 64, 665–666
16 Ruxton, G.D. *J. Anim. Ecol.* (in press)

Reply from J. Bascompte and R.V. Solé

The above comment is the latest round in a running argument about a technical subject concerning the way in which dispersal is formulated and how it affects local dynamics. We are afraid that such comment does not add to the published discussion, and we suggest that readers refer to previous discussion[1,2] or even our own review in *TREE*[3], where we tried to address all of this controversy (see our Box 2).

We agree with Rohani and Ruxton that some of the modelling aproaches used by us are a little simplistic, and that the role of dispersal in local dynamics can depend on the specific dispersal rule. Further work is necessary, as we emphasized in our prospects section. However, Rohani and Ruxton adopt an extreme position. Their statement that our previous results emerge solely as a result of our unrealistic dispersal rule should be tempered. The references cited in their comment relating to our early work describe many results as the emergence of spatial patterns or the coexistence of competitors mediated by space, which have been found simultaneously by other authors using other modelling rules (see references in our *TREE* review). Even when Rohani and Ruxton refer to the specific issue of diffusion-induced chaos, claiming that such a destabilizing mechanism does not transfer to discrete models, their statement should again be tempered. As pointed out recently in this journal in a reply to Ruxton's first comment[4] by Hastings and Higgins, the extensive study of a discrete time model shows unequivocally that spatial degrees of freedom 'allowed for even more complex behaviour to emerge than was found in models that did not incorporate spatial dynamics'[5]. Furthermore, this result was obtained adopting the dispersal rule used by Rohani and colleagues[1].

To sum up, the comment by Rohani and Ruxton is useful in exploring more realistic scenarios, in adopting a critical re-examination of results, and in suggesting further studies. At the moment,