Phylogenetics and speciation

Timothy G. Barraclough and Sean Nee

Species-level phylogenies derived from molecular data provide an indirect record of the speciation events that have led to extant species. This offers enormous potential for investigating the general causes and rates of speciation within clades. To make the most of this potential, we should ideally sample all the species in a higher group, such as a genus, ensure that those species reflect evolutionary entities within the group, and rule out the effects of other processes, such as extinction, as explanations for observed patterns. We discuss recent practical and theoretical advances in this area and outline how future work should benefit from incorporating data from genealogical and phylogeographical scales.

SPECIATION (see Glossary) is the creative process leading to the build up of species diversity; understanding the general patterns and processes of speciation is fundamental to explaining the diversity of life. Central questions include what are the general causes of speciation, and how do rates of speciation vary over time and among taxonomic groups and geographical regions? Although fundamental, such questions are difficult to answer because direct observation is usually impossible and many extant groups do not have adequate fossil records with which to investigate these topics (but see Benton and Pearson, this issue).

The expansion of molecular PHYLOGENETICS over the past decade has opened up a powerful new approach to this problem. PHYLOGENETIC TREES, particularly those including all the living species in a higher taxonomic group, provide an indirect record of the speciation events that have led to present-day species. Together with information on the geographical and ecological attributes of species, they can provide information on the causes of speciation within the group. In addition, trees derived from DNA sequences contain information about the relative timing of reconstructed speciation events, and can be used to estimate speciation rates.

This has led to considerable interest in molecular phylogenetics as a tool for solving speciation problems, but success rests on two fundamental issues. First, the approach relies on reconstructing evolutionary species relationships within a clade. Few biologists deny that the evolutionary entities referred to as species do exist, but the taxonomically recognized species in a clade might not correspond to those entities (see Hey, this issue). Second, processes in addition to speciation influence the phylogeny and attributes of present-day species.

For example, species are lost by extinction, and subsequent phenotypic evolution might obscure the ecological pattern of speciation events. Hence, a phylogenetic tree cannot simply be read as the history of speciation: analyses must factor out alternative processes as explanations for observed patterns.

Our review discusses recent progress in this area. We discuss methodological issues in reconstructing species histories, and move on to the two broad questions concerning the rates and causes of speciation. Finally, we consider the future possibilities of incorporating fine-scale genealogical data into large-scale phylogenetic studies.

Species-level phylogenies

Phylogenetic studies of speciation have focused on reconstructing species-level phylogenies, namely the relationships among species within higher groups such as genera. The internal nodes of the tree reflect speciation events: it is known 'who split from whom' and, ideally, the timing of those events. Because reconstruction relies on living species, there is no record of speciation events involving species that subsequently went extinct, although extinction can leave a signature on the shape of the tree. Phylogenetic reconstruction from molecular data is an advanced science, but two issues have been particularly important when applying phylogenetics to studies of speciation.

The first is the issue of sampling. To obtain an accurate view of speciation in a higher group, nearly all the species from that group should be sampled. Missing species reduce the sample size of reconstructed speciation events available, and can introduce bias, for example by tending to remove the most recent speciation events or those involving rare species. In particular, the ability to consider the effects of other processes, such as extinction, on the observed patterns relies crucially on a very complete sample of species. However, most phylogenetic studies do not sample all the described species within a group, and, for reasons outlined in Box 1, special effort can be required to do so.

The second issue relates to the status of species included in phylogenetic trees. Most phylogenetic studies of higher clades sample one individual from each species named in the checklist for the group. Using the resulting tree to study speciation assumes that taxonomic species generally reflect the evolutionary entities whose origin we wish to explain, but this need not be so. The number and identity of taxonomic species in a group depends upon the judgement of the taxonomist who described them, and opinions can vary (the infamous splitting-lumping continuum). More fundamentally, it might not always be possible to resolve the true history of speciation into a tree of monophyletic species, because some modes of speciation lead to paraphyletic species or even phylogenetic...
Box 1. Reconstructing species-level phylogenies

Several methodological problems have faced researchers wanting to reconstruct species-level phylogenies for studying speciation. The first is obtaining DNA from all the species of a sufficiently large monophyletic group to detect any patterns. Collection of DNA from rare species might be difficult or impossible and it might be hard to guarantee PCR amplification from every species using universal primers. Statistical methods exist to investigate incomplete samples of species, but complete samples will still be needed to detect many patterns. Second, even if samples can be obtained, it might be difficult to obtain a fully resolved tree. Many existing DNA regions were developed for higher level systematics and might evolve too slowly to resolve the species level. Faster evolving regions are available, but can have associated problems, such as the existence of alternative multiple copies or the difficulty of using universal primers in the chosen target group. Alternative methods are being explored, such as genetic fingerprinting techniques or the use of transposable elements.

Alternatively, we might have to accept that 100% resolution is not always possible at this level, and develop analytical approaches that take uncertainty into account. For example, Bayesian approaches are being developed that allow estimation of evolutionary parameters, such as speciation and extinction rates, as an integral part of the phylogeny reconstruction process, taking account of uncertainty in the tree. Finally, existing studies are usually limited to a single exemplar for each described species in a group, and to one or a few molecular markers. Several processes can complicate reconstruction of species history from the resulting gene trees, including modes of speciation producing paraphyletic species, lineage sorting of ancestral polymorphisms and hybridization. Genealogical methods based on reconstructing multi-gene trees and sampling larger numbers of individuals per named species are available to cope with these issues. These approaches allow accurate reconstruction of species histories, but to date have been too time-consuming or costly to apply to studies of large groups. Aside from difficulties of collection, the above problems are becoming less severe as molecular methods become faster and cheaper, making it easier to obtain comprehensive samples for multiple genes within clades.

References


Estimating speciation rates

A central question concerning speciation within clades relates to how often speciation occurs. A large literature has developed describing methods for estimating speciation rates from trees containing all the species within a clade. These methods use information on the time elapsed between successive branching events, and can be illustrated graphically by plotting the number of lineages through time (Fig. 1). If speciation rates have been constant over time and among lineages, and there has been no extinction, a straight line with slope equal to the average per lineage speciation rate, b, is expected (Fig. 1).

This approach has been used to estimate the average speciation rate during the radiation of Hawaiian silverswords (family Asteraceae). This plant group has diversified into a wide range of taxa on the archipelago, from cushion plants and vines to trees. Using an inferred maximum age for the divergence between silverswords and their Californian sister clade, a minimum per lineage speciation rate of 0.56 ± 0.17 species my⁻¹ was estimated. This suggests that the silverswords have speciated at rates comparable to peak origination rates observed from fossil evidence during continental radiations.
Box 2. Dating phylogenies

DNA sequence data can be used to estimate the relative ages of nodes on a phylogeny. Assuming that nucleotide substitutions between taxa accumulate randomly over time, molecular distances reconstructed onto the phylogeny are expected to be roughly proportional to the time elapsed. However, variation in substitution rates among lineages means that we cannot assume a strict molecular clock in most cases. Recently, a variety of methods have been proposed for estimating the relative ages of nodes, with confidence intervals, from sequence data even in the absence of molecular clock. Most are likelihood methods that fit node ages under explicit or heuristic models of how rates change among lineages. The exception is Sanderson's Non-Parametric Rate Smoothing algorithm, which converts an unconstrained tree (in which branch lengths reflect rate as well as time) into an ultrametric tree (in which branch lengths only reflect time) by minimizing rate changes across the tree. These methods have not yet been fully evaluated on real data, but represent an important step forward. Additional complexities can arise when considering very recent speciation events, in which genetic diversity within populations can have a large effect on estimates of divergence times (see Nichols, this issue).

Calibration of the tree in real time remains difficult, relying on the availability of fossil dates or biogeographical evidence, which can be lacking in some groups. The traditional approach of using blanket calibrations for rates of molecular evolution, such as the widely used insect mitochondrial DNA clock of 2% pairwise sequence divergence per million years, is confounded by rate variation among taxa. However, more sophisticated calibrations should be possible in future, using tests for rate variation between study groups and reference clades with calibrated dates. This will rely on the availability of a library of well-dated phylogenies derived from commonly used genes.

References


The situation is more complicated if the data are not consistent with a constant speciation rate model. For example, extinction occurring randomly and at a roughly constant rate over time is expected to cause an apparent acceleration in speciation rate towards the present (Box 3). In this case, it is possible to estimate speciation and extinction rates separately, rather than just to estimate the net DIVERSIFICATION RATE. However, as described in Box 3, other processes, and sampling and taxonomic artefacts in particular, can affect the shape of the plots. Estimates of speciation rates and their interpretation rely heavily on these issues. Nonetheless, although the outcomes of some processes might be statistically indistinguishable, the range of diversification models consistent with the data can be narrowed down, thereby gaining better estimates of speciation rates.

At present, few studies have applied these techniques to estimating speciation rates in real clades, possibly mainly because of the rarity of sufficiently complete trees. As more data become available, particularly those demonstrating the evolutionary status of included species, variations of these methods will be used for broad surveys of speciation rates. In addition, links between genealogical approaches and the methods we describe should allow estimation of a broader range of parameters, such as the relative rates of paraphyletic and monophyletic modes of speciation,
Box 3. Departures from the constant speciation rate model

Several processes can lead to departures from the expectations of the constant speciation rate model outlined in Fig. 1. An apparent increase in speciation rate towards the present, as found in the Elipsoptera group of tiger beetles (Fig. I), can be caused by: (1) an actual increase in the speciation rate, or (2) an illusory increase caused by a constant background extinction rate, d, that is high relative to the (constant) speciation rate, b (Ref. b). In the latter case, the slope near the present asymptotically approaches the speciation rate, whereas the slope in the main body of the graph equals speciation minus extinction rate (i.e. the net diversification rate). The two explanations might be distinguishable in some circumstances. The upturn as a result of extinction is expected to start at around 1/(b−d) time units before the present, whereas, for example, if speciation rates increased during the Pleistocene we expect an upturn within the past 2.5 million years. The predictions will differ for clades with b−d <0.4 species per million years. In the tiger beetles, the upturn is more recent than expected because of a constant background extinction rate.

A slowdown in the diversification rate towards the present, as found in New World warblers of the genus Dendroica (Fig. II), can be caused by a decrease in speciation rate or an increase in extinction rate. If background extinction has occurred in the group, we would expect to see a recent upturn above the levelling off stage, but beyond that it is probably not possible to distinguish the two explanations.

Sampling artefacts can also influence the patterns we observe. Phylogenies reconstructed from an incomplete sample of species tend to underestimate the number of nodes towards the present, creating an apparent slowdown. Methods exist to evaluate the impact of known missing species, assuming those species comprise a random sample. However, over-splitting or lumping by taxonomists could also lead to artefactual upturns or slowdowns respectively, if taxonomic species are used as terminals.

Finally, the analyses are sensitive to any biases affecting the methods used to reconstruct node ages. For example, multiple substitutions at the loci used to build the phylogeny could lead to saturation of genetic distances, producing shorter branch lengths deeper in the tree. Maximum likelihood and some distance methods can be used to avoid this problem, but there has been little general work on how methods for reconstructing branch lengths and node ages might bias analysis of diversification rates.

References
c Harvey, P.H. et al. (1994) Phylogenies without fossils. Evolution 48, 523–529

and the frequency of hybrid speciation. Even without these extensions, the approach offers a means to investigate otherwise unanswerable questions in groups lacking fossil records.

Changes in speciation rate over time
Speciation rates change over time for a variety of reasons and the methods described can be extended to test for such changes. For example, one widespread hypothesis is that glacial cycles during the Pleistocene (2.5 to 0.01 million years ago) increased speciation rates in Northern Hemisphere groups (25,26). The main evidence for this is that many species and populations display genetic divergences from their nearest relatives consistent with separation during the late Pleistocene. However, even if speciation rates remained constant, it is expected that many divergences would be clustered towards the present. It is therefore vital to test for a significant increase in speciation rate during the Pleistocene compared to the null model of constant speciation rate. Such a test was performed using mitochondrial DNA phylogenies of 11 lineages of passerine birds (27). It was found that net diversification rates decreased towards the present rather than increased, contrary to the predictions of the Late Pleistocene origins hypothesis.

Many studies have used similar patterns to argue that diversification rates typically decline during the radiation of clades (28,29). This might occur because the opportunity for speciation decreases as ecological or geographical space becomes filled (30), or as a consequence of decreased range sizes following successive subdivisions of ancestral ranges (31). However, several artefacts can also create the illusion
of early bursts of ‘explosive’ speciation. These include incomplete sampling, taxonomic underestimates of the number of evolutionary species, and possible biases in estimates of node ages (Box 3). Even if none of these problems apply, it might be impossible to distinguish falling speciation rates from rising extinction rates\(^\text{32}\).

**Variation in speciation rate among regions**

Species richness varies widely among regions, but what causes hotspots of diversity? Phylogenetic data can provide insights into this problem. For example, studies in South American and African tropical birds have used phylogenetic data to infer precisely where in the tropics the most recent speciation occurred\(^\text{33,34}\). In both cases, they concluded that the phylogenetically youngest species do not tend to be found in the central areas of lowland rain forest, but rather in the surrounding topographically complex, montane areas. This appears to rule out lowland areas as hotbeds of recent speciation.

With complete species-level phylogenies for study groups, it should be possible to estimate how speciation and extinction rates vary among regions. One example is the recent investigation of the evolutionary basis of a species–area relationship, by comparing speciation rates of Anolis lizards among Caribbean islands of different sizes\(^\text{35}\). Future studies could apply similar approaches in continental regions and at a global scale. For example, does high speciation and/or low extinction explain the occurrence of floristic hotspots in Mediterranean climate regions\(^\text{36}\), and, what are the relative roles of speciation and extinction in causing latitudinal gradients in species richness\(^\text{37}\)?

**Variation in speciation rates among taxa**

Speciation rates of taxa might depend on their biological characteristics, such as body size or the degree of sexual selection. To date, most tests of such hypotheses have made only limited use of phylogenetic information, simply comparing the numbers of species in sister taxa that differ in the trait of interest\(^\text{38}\). As a result, it cannot be ruled out that extinction, rather than speciation, might have caused the observed patterns. As more species-level phylogenies become available, it will be possible to estimate speciation and extinction rates separately for multiple sister taxa pairs. Similarly, it might be possible to test for the effects of rapidly changing traits on speciation rates, even in the absence of sister taxa differing unambiguously in their expression of the trait\(^\text{39}\). For hypotheses where the effect of the trait is uncertain, such as body size, these tests will be crucial in narrowing down possible mechanisms.

**Causes of speciation**

Perhaps the most fundamental question in the study of speciation is what causes a single ancestral species to split into two (or more) daughter species? The traditional evidence for answering this has been to look at recently split species to infer what processes might have been important. For example, evidence that sexual selection can play a key role in speciation initially came from observations of large differences in secondary sexual traits among closely related species\(^\text{40}\). Molecular phylogenetics allows more precise tests: species relationships can be more accurately known and information on the timing of speciation allows us to focus on the most recent events. However, a key limitation with this approach is that changes can occur since speciation: any patterns observed for even closely related species could be the incidental outcome of the independent evolutionary histories of those species, rather than indicative of the forces promoting speciation\(^\text{41,42}\). Also, extinction can affect the characteristics displayed by surviving species. Hence, some way is needed to factor out the effects of incidental change and extinction on the patterns observed. We discuss two areas now exploring this approach.

**Geographical isolation**

Several authors have used species-level phylogenies to assess the relative frequencies of different geographical modes of speciation, based on the geographical distributions of recently formed sister species\(^\text{43,44}\). For example, in a recent study of several bird, insect and fish species\(^\text{41}\), all of the most recent splits had no range overlap, suggesting that allopatric speciation is the norm (with some possible exceptions). Also, range size differences between recently split species suggest that speciation often involves the isolation of small populations, so-called peripatric speciation. Other measures can be used to explore other modes, such as the frequency of parapatric speciation, or the role of external boundaries, such as rivers and mountain ranges\(^\text{42}\).

The Achilles heel of these studies is that ranges of species can move, even over very short timescales. If range movements are common, present-day ranges might not preserve a record of the mode of speciation. In the above study, several clades showed the same qualitative pattern of range overlaps as would be expected if species ranges had moved to random locations within the area occupied by the whole clade\(^\text{44}\). Recent work has tried to deal with this problem in several ways: (1) by looking at situations where range movements are unlikely to cloud the results, such as speciation on small oceanic islands; (2) by checking the success of biogeographical methods in cases known to have a particular mode of speciation, for example, presumed sympatric speciation of polyploid plants; or (3) by proposing tests for historical signals, for example, randomizing ranges of species among the tips of the phylogeny and comparing observed overlaps of sister species to those obtained between random pairs of species\(^\text{41}\). Although choosing a realistic null model can be difficult\(^\text{44}\), the third approach could offer a general way forward.
Box 4. Character shifts and speciation

The locations of shifts in ecological characters can be reconstructed onto a tree using maximum parsimony or likelihood methods. Figure 1 shows a hypothetical example of a clade with three reconstructed changes (marked by vertical bars) in the state of a discrete character. If ecological shifts occur incidentally over time with no effects on speciation or extinction, we expect shifts to be distributed across the phylogeny roughly in proportion to the time available for them to occur, that is, the branch lengths of the tree. If shifts are associated with speciation, we expect to see: (1) more ecological differences between recently split species than expected, given average rates across the tree and the short divergence time of those splits; and (2) that the amount of change within lineages is more directly proportional to the number of nodes than to branch lengths. If ecological differences are associated instead with the long-term persistence and subsequent radiation of lineages, we might expect that most shifts would be observed between more distantly related lineages within the clade.

Any test of these predictions must take into account that the location of shifts are reconstructed and are therefore prone to uncertainties or biases of the reconstruction method. Other discrete or continuous species traits thought to be involved in speciation, such as reproductive morphology or genetic characters, could be treated in the same way.

References


Also, tests for particular modes can look at additional predictions, for example that peripatric speciation should lead to imbalanced trees or that sympatric speciation should involve host shifts. Extinction can also affect geographical patterns, but its effects have been little explored. Random extinction occurring at a constant rate over time tends to prune older lineages, leaving many recent speciation events ‘untouched’, and therefore could have a fairly minor effect. However, selective extinction, for example for species with smaller ranges or those that interact with large numbers of close relatives, could have a much larger effect, perhaps even biasing evidence for geographical modes. Another source of bias might come from taxonomic artefacts, for example if taxonomists were more likely to recognize taxa as species when they are sympatric with their siblings.

Despite the problems, phylogenetics provides a framework for considering the effects of other processes and has led to refinements of existing tests. Further refinements should come when phylogeographical data are available for all the species in a higher clade. This should make it possible to determine, for example, what proportion of populations go on to form reproductively isolated and morphologically recognizable species, and what distinguishes the winners from the losers.

Ecological shifts

Recent work has renewed interest in the role of ecological shifts in speciation, and phylogenetics provides a means to test the generality of these findings at scales where detailed experiments are not possible (see Schluter, this issue). The basic approach is to map ecological characters onto a tree (Box 4), with the prediction that recently split species will tend to occupy different niches or habitats. For example, a large body of work on herbivorous insect groups has shown that closely related species are often found on different host-plant species. Similarly, phylogenetic evidence supports a possible role of habitat shifts in several Hawaiian groups, including silversword plants, Drosophila, and spiders from the genus Tetragnatha. However, except in the most extreme cases, there is again the problem that ecological differences between even closely related species could have evolved since speciation, as a by-product of independent evolutionary history.

One solution is to compare observed ecological differences among species to those expected under a null model in which ecological traits evolve randomly through time with no effect on speciation (Box 4). This approach is stricter in the criteria needed to demonstrate that ecological shifts are linked to speciation, but there remain limitations. Characters that change predominantly at speciation events need not play a causal role in the speciation process; the evolution of some characters might be speeded up by conditions during speciation, such as small population size. Also, even using null models it might be difficult to distinguish rapidly evolving characters from those involved in speciation. Hence, theoretical and experimental evidence is vital for supporting the hypothesis that a given trait is involved...
promoting reproductive isolation and diversity in sexually selected characters? What role do genetic processes, such as changes in chromosome number, gene rearrangements and duplications, play in speciation? Considering the evolution of genetic characters with respect to phylogeny will allow estimates of the relative frequencies of different types of change and tests for their intimate association with speciation. Work on these questions has already started, but major advances should be seen over the next few years, as more complete reconstructions of evolutionary relationships in clades become available.

Linking genealogical and phylogenetic scales

The previous discussion has shown how broad-scale phylogenetic studies can help to identify general trends in speciation, but a potential weakness to date has been that most studies at this level rely on taxonomic species as surrogates for evolutionary species. Current technology for DNA sequencing means it is becoming feasible to sample genealogies of individuals within all the species of a higher taxonomic group, such as a genus. These data will allow tests of the validity of using taxonomic species in speciation studies, but more importantly will allow a broader range of questions to be answered. By identifying boundaries between evolutionary species, it will be possible to ask what features are associated with species boundaries, whether the multifarious aspects of species tend to evolve in concert, and what role the external environment plays in producing genetic and phenotypic clusters.

Two areas would seem particularly hard to address without integrating genealogical and phylogenetic approaches: the role of hybridization in speciation, and speciation in asexually reproducing lineages.

Hybridization and speciation

Hybrid speciation occurs when hybridization between two species leads to the formation of a new, third species. It has been long considered important in plants, with 11% of plant species richness attributed to this mode by recent authors, but it might also play a role in animals. The main tool of current research is detailed genetic analysis, but phylogenetics could play a key role in the future resolution of the general prevalence of hybrid speciation. Current work suggests two ways in which such tests might proceed. First, extensions of traditional methods of phylogeny reconstruction could be used to reconstruct detailed histories of hybridization and cladogenesis in terms of networks. As yet, the practicalities of this approach for large data sets are uncertain: allowing for lateral connections among taxa increases the number of possible solutions among which to search for the optimum. The second approach is to estimate the frequency of hybridization without reconstructing
an explicit history of those events. Current methods have been developed to quantify levels of recombination among groups of bacterial and fungal sequences, but similar tests could be applied to hybridization between species. A problem common to both approaches is that it might be hard to distinguish hybrid formation of a new species from gene flow between two existing species that does not lead to formation of a third species.

Asexual speciation?

Sexual reproduction might explain the existence of the discrete units recognized as species: interbreeding maintains coherence within populations, whereas reproductive isolation leads to genetic and phenotypic discontinuities among isolated populations (see Turelli et al., this issue). However, if similar genetic and morphological clustering were found in asexual taxa, external ecological factors might be more important than is sexual reproduction in explaining why species exist. One way to test this idea would be to compare genealogical histories between closely related sexual and asexual taxa. The data could be used to: (1) identify whether discrete genetic and morphological clusters exist in asexual taxa; (2) test whether the degree of clustering is more extreme than expected simply from a stochastic birth–death model of asexual division; (3) compare the rate of origin of observed clusters between sexual and asexual taxa; and (4) test what role divergent selection from environmental variables might play in the process.

Conclusions

Our aim has been to show the enormous potential of molecular phylogenetics for answering long-standing questions about speciation. Current studies have been caught between the competing demands of sampling enough species to detect any patterns and establishing the evolutionary status of the included species. It can still be difficult to reconstruct an accurate species phylogeny for higher groups, but ongoing practical and theoretical advances are making it feasible to meet both demands in a single study. Even so, there is still the need for studies that sacrifice detail for scale, and vice versa.

Assuming a suitable tree is available, theoretical questions remain about how best to extract information on speciation and in particular how to rule out the effects of other processes such as extinction. The basic theory on rates of speciation is well established, but extensions are needed to answer questions at finer and broader scales, for example, what proportion of populations go on to form fully fledged species, and how does the probability of speciation vary geographically? The theory for investigating the causes of speciation is much more diffuse, and a stronger framework is needed before the generality of mechanisms outlined in this special issue can be firmly assessed. Crucially, ways are needed to identify when the signal of speciation has been lost entirely from present species.

Finally, we have outlined how major advances over the next few years will probably result from bridging the gap between genealogical and phylogenetic scales. Genealogies allow accurate reconstruction of species histories and insights into population processes, but a phylogenetic perspective is needed to identify general trends and to consider the full array of processes leading to species diversity within cladades.

References

10 Nee, S. On inferring speciation rates from phylogenies. Evolution (in press)


39 Darwin, C. (1871) The Descent of Man and Selection in Relation to Sex, John Murray


---

**TREE online - making the most of your personal subscription**

High quality printouts (from PDF files)
Links to other articles, other journals and cited software and databases

To claim your FREE online access to Trends in Ecology and Evolution:

Go to http://www.bmn.com/general/subkey and select Trends in Ecology and Evolution from the list
Enter your own BioMedNet login details when prompted (if you are not yet a member, joining takes minutes and is FREE)
Follow the instructions on the Trends in Ecology and Evolution page under ‘Personal Subscriber Access’

You only need to register once.

For subsequent visits, bookmark: http://journal.bmn.com

**Tip:** If you do not use a shared terminal, you can tick the ‘save password’ box when you first log on to BioMedNet so that you only need to register once

If you have any questions e-mail: info@current-trends.com

---

http://tree.trends.com