

Complex interactions between plant diversity, succession and elevated CO₂

Considerable optimism and a certain disdain for all things past are distinctive characteristics of quickly developing fields of science. This is true of research into plant responses to elevated atmospheric CO₂ and on biodiversity effects on ecosystem processes, both areas of research that have tended to ignore both each other and some fundamental community processes that are well understood within the framework of traditional plant ecology. Highly simplistic experimental arrangements and strong responses to treatments – sometimes leading to dramatic projections to the real world – were characteristics of early studies in both areas.

Recently, there has been an increased interest in moving into more realistic growth conditions and plant assemblages, based on accumulating evidence that responses of natural systems tend to be strongly influenced by resource conditions, plant traits and interactions, and might involve complex positive and negative feedbacks. The recent article by Pascal Niklaus and colleagues¹ is a rare example of this new research trend.

Together with Reich *et al.*², Niklaus *et al.*¹ are one of the first to show bi-directional interactive effects of elevated CO₂ and plant diversity on plant community productivity. The authors tested whether the ecosystem responses to elevated CO₂ changed when

specific sets of species were lost from nutrient-poor calcareous grasslands. They set up a five-yr field experiment in northwestern Switzerland, constructing communities composed of five, 12 and 31 plant species assembled from the native species pool, and submitting them to either ambient or elevated atmospheric CO₂.

As reported elsewhere², Niklaus *et al.* found that diversity influenced plant-community response to CO₂ enrichment. Elevated CO₂ increased biomass production only in communities with the highest number of species. Interestingly, as recently established communities, the assemblages underwent compositional changes during the experiment. Following a classic secondary succession process, there was a gradual replacement of fast-growing short-lived species by slower-growing, conservative species. At different successional stages, increased biomass production by elevated CO₂ in more diverse communities was due to the presence of responsive species that were absent in species-poorer communities, and these responsive species were different at different successional stages. This suggests that, although response to elevated CO₂ is more dependent on plant species traits than on species number, a rich species pool might be important to maintain high productivity under changing environmental conditions.

CO₂ enrichment also affected biodiversity. Elevated CO₂ altered succession by reducing species extinction and increasing coexistence between early- and late-successional species. The fact that elevated CO₂ might slow down secondary succession is relevant in a world where disturbance makes early-successional communities increasingly common.

The findings of Niklaus *et al.* might be bad news for those wishing to obtain simple principles to predict the future. Species composition is unlikely to be just a passive response variable in the face of global change. Self-feeding, non-linear processes can occur, with different communities having different responses to CO₂ enrichment, and elevated CO₂ affecting the composition of these communities. However, this article shows how fruitful it can be to integrate CO₂ and biodiversity research in long-term studies, and combine cutting-edge enquiry with good old-fashioned natural history.

1 Niklaus, P.A. *et al.* (2001) A long-term field study on biodiversity x elevated CO₂ interactions in grassland. *Ecol. Monogr.* 71, 341–356

2 Reich, P.B. *et al.* (2001) Plant diversity enhances ecosystem responses to elevated CO₂ and nitrogen deposition. *Nature* 410, 809–812

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Age before beauty: male flies prefer long-lived females

The issue of which indicators animals use as the basis for choosing a mate has been at the heart of evolutionary biology since its inception. In most cases, females are the choosy sex, and this is evident in the enormous array of sexually selected traits that male animals display. However, on the rare occasions where the supply of females outstrips demand, males get to choose. In such cases, males normally favour fecundity (or a correlate, such as body size). However, a recent paper by Derek Dunn and colleagues¹ suggests that males of the seaweed fly *Gluma musgravei* (Diptera: Coelopidae) choose females not on the

basis of how many eggs they have, but on their future longevity. This is the first demonstration in any species of a male preference for future survivorship in a mate.

In coelopid flies, females struggle against males that try to mount them by kicking, shaking or curling their abdomen, and larger males are better able to overcome this resistance. In spite of what are probably considerable costs of overcoming female resistance, males often dismount a pacified female without copulating. Dunn *et al.* found that similar aged females rejected in this way had a lower future survival than did those that

males accepted. Even after an association between female size and life span was controlled for, males were found to be discriminating against shorter-lived females before attempting a mating. The exact mechanism of discrimination is still unclear, but, as the authors suggest, males might be able to assess potential female longevity by differences between individuals in their resistance behaviours. Males do not pass beneficial substances to females during copulation that might enhance female longevity. In fact, it is more common in dipteran flies for copulation to decrease female life span. Resistance to mating is

testament to the probable costs to females of mating, and therefore differences in longevity between these females are not a result of mating.

But why do these males assess females on the basis of their future life expectancy? Seaweed flies, as the name suggests, lay their eggs in seaweed deposits that get washed up above the high tide mark on beaches. Such deposits are highly ephemeral and the longer the post-mating

survival of the female, the more likely she is to successfully lay her eggs. By choosing longer lived females, males are maximizing their chances of successfully leaving offspring. This is especially important in a mating system that is characterized by costly sexual conflict – by expressing such a choice males are best able to allocate their time and resources to reproduction. This example of sexual selection for longevity has important

implications for the trade off between fecundity and life span, and future studies should consider these.

1 Dunn, D.W. *et al.* (2001) Male mating preference for female survivorship in the seaweed fly *Gluma musgravei* (Diptera: Coelopidae). *Proc. R. Soc. London B Biol. Sci.* 268, 1255–1258

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Getting it right for the wrong reason

A statistical framework is necessary for almost every scientific field, but few disciplines had as much trouble as phylogenetics did in establishing one. The long and frustrating arguments over different methodologies and philosophies (cladistics versus phenetics versus evolutionary taxonomy in the earlier years – cladistics versus statistical inference more recently) might have waned but their echo still reverberates. In a short historical essay¹, Joe Felsenstein, one of the principal architects of the 'statistical revolution' in phylogenetics, tells the story of the growth of a much-troubled field with characteristic clarity and vigour. Those interested in the way that science (and scientists) proceeds and advances will find the essay illuminating, not least because it offers a nice illustration of a paradigm-shift in the making.

However, criticisms against statistical phylogenetic inference still remain.

Swofford *et al.*² have now addressed one of the latest criticisms levelled against model-based methods (and particularly likelihood); the notion that parsimony outperforms likelihood in reconstructing topologies belonging to the area of tree space known as the 'inverse-Felsenstein zone', which comprises trees with two long branches that are adjacent (Fig. 1a). This is exactly the reverse of the 'Felsenstein zone', the area of tree space where the two long-branched taxa are separated by a short internal branch (Fig. 1b). In Fig. 1b, likelihood outperforms parsimony, the latter producing strong support for the wrong tree. In both zones, the outcome from likelihood analysis is a star phylogeny (Fig. 1). Understanding the reasons behind potential biases of particular methods in the two zones is biologically relevant and significant; a glance at the phylogenetic literature of early eukaryotes will be convincing enough.

Swofford *et al.* demonstrate convincingly that the reason behind the success of parsimony in the inverse-Felsenstein zone is the same for its failure in the Felsenstein zone. Homoplasies (i.e. parallel or convergent changes) are treated as homologies (i.e. changes revealing identity by descent), owing to the inability of parsimony to correct for multiple substitutions (red dots in Fig. 1). The extent of bias can only be appreciated in a numerical example. In the case of a four-taxon unrooted tree where there have been, on average, two changes in each of the two long branches and 0.2 changes on each of the three short ones, 97% of all apparent homologies will be misinterpreted homoplasies. It is perhaps an understatement to say that researchers will feel uncomfortable about their pet phylogenies after reading these values. By contrast, the star phylogenies produced by likelihood are a consequence of the low support of the data for the 'true' phylogeny, given that very few changes have happened on the short internal branch. Swofford *et al.* also show that UPGMA, a phenetic method whose assumption of an equal rate of change in all lineages is violated in both cases, is behaving in almost exactly the same manner to parsimony in the two zones. I doubt that parsimony advocates will find this last finding exonerating.

1 Felsenstein, J. (2001) The troubled growth of statistical phylogenetics. *Syst. Biol.* 50, 465–467

2 Swofford, D.L. *et al.* (2001) Bias in phylogenetic estimation and its relevance to the choice between parsimony and likelihood methods. *Syst. Biol.* 50, 525–539

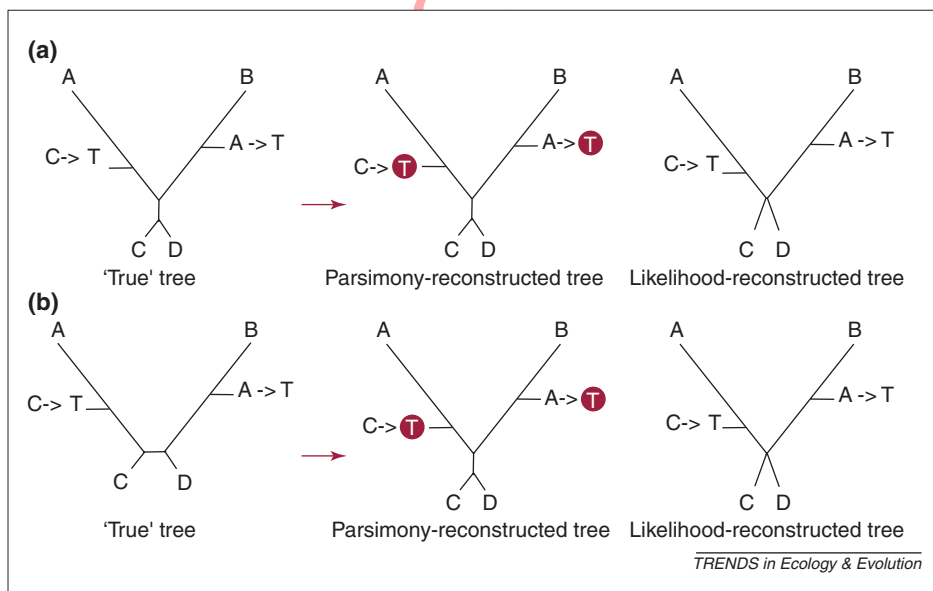


Fig. 1. Behaviour of parsimony and maximum likelihood in the (a) 'inverse-Felsenstein zone' and (b) 'Felsenstein zone'. Red dots indicate homoplasies that are mistakenly identified as homologies by parsimony.

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Alternative reproductive tactics and sexual selection

Alternative reproductive tactics within the sexes are common in nature and often involve a territorial, courting tactic and a nonterritorial, sneaking tactic. The evolution of such tactics is generally thought to increase the variance in reproductive success and thus increase the opportunity for sexual selection. Therefore, mating systems with alternative reproductive tactics should have an associated exaggeration of sexually selected characters, such as body size (e.g. as measured by sexual dimorphism), the development of weapons (e.g. horns) or costly ornaments (e.g. colourful, conspicuous badges). This paradigm has become an integral part of sexual selection theory, and has received widespread support, particularly from results of avian studies. For example, in many bird species, the frequency of sneaking (or extra-pair fertilizations) is positively correlated with the development or exaggeration of sexually selected traits in males, such as plumage brightness, ornament and body size. However, a new model and empirical data¹ from a fish suggest that such a link between the presence of alternative reproductive tactics and an increase in the opportunity for sexual selection might not be so straightforward.

Adam Jones *et al.*¹ have recently developed a mathematical model that

incorporates not only the frequency of territorial (nesting) and sneaking behaviours, but also allows for individuals to utilize each tactic to a varying degree. They show that when most individuals employ one tactic, for example a nesting tactic, whilst a few individuals successfully employ both tactics (e.g. nesting and sneaking), the opportunity for sexual selection increases. This result is consistent with the many avian studies conducted on species that are usually socially monogamous, but some nesting males successfully steal fertilizations from neighbouring nesting males through a 'sneaking' tactic. Alternatively, Jones *et al.*¹ show that when there is a discrete reproductive polymorphism, for example when some individuals employ only the nesting tactic, whilst others employ only the sneaking tactic, sneaking can, in many cases, decrease the opportunity for sexual selection (as compared to a mating system in which the sneaking tactic had not evolved). Jones *et al.*¹ use a genetic analysis of paternity to track the relative frequency and success of sneaking and nesting tactics in sand gobies *Pomatoschistus minutus* and show that, based on their model, sneaking has in fact reduced the intensity of sexual selection.

Of paramount importance will be demonstrating that the evolution of an

alternative reproductive tactic, such as sneaking, has reduced the opportunity for sexual selection in a population as measured by the response in sexually selected characters. This could be accomplished by examining the appropriate characters across multiple populations that differ in the proportion of individuals that utilize the sneaking tactic in a species that is characterized by a discrete reproductive polymorphism. Populations with a greater proportion of specialized sneaker individuals should have less exaggerated sexually selected characters. For example, if nesting males had a secondary sexual trait, such as a colourful badge, then the size or intensity of this badge should be inversely related to the frequency of sneaker individuals. Interestingly, although discrete reproductive polymorphisms can generally decrease the opportunity for sexual selection, intense sexual selection could be a precursor for the evolution of these polymorphisms.

1 Jones, A.G. *et al.* (2001) How cuckoldry can decrease the opportunity for sexual selection: data and theory from a genetic parentage analysis of the sand goby, *Pomatoschistus minutus*. *Proc. Natl. Acad. Sci. U. S. A.* 98, 9151–9156

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Straining for a net profit

Pelagic tunicates (salps, appendicularians, pyrosomas and doliolids) are gelatinous marine zooplankton that are common in most of the oceans of the world. These animals are extremely successful, having colonized the nutritionally poor oceanic 'blue water' areas and abyssal depths, and are capable of producing dense populations that mediate massive fluxes of fecal material from the surface to the deep sea. This transformation of planktonic carbon into 'marine snow' is an important part of the role of oceans as an atmospheric carbon sink. However, in spite of their ecological importance, relatively little is known about these animals. Perhaps most intriguing are their relatively large, transparent gelatinous bodies. Recently, José Luis Acuña¹ has shown that the strange, gelatinous bodies of these pelagic tunicates are essential to their ability to thrive in nutritionally poor habitats.

Although they have energy requirements that are similar to other zooplankton with the same carbon content, pelagic tunicates are able to maintain normal feeding and swimming behaviours in ultraoligotrophic areas, and during seasonal periods of food scarcity in temperate seas, without resorting to dormant stages or diapausing eggs. Acuña links a previous suggestion, that gelatinous zooplankton can develop large and delicate feeding structures because of the reduced gravitational and turbulent shear stresses in their natural environment, with filtration theory to provide an answer to the success of the tunicates. By combining theory and empirical data on their physiology, Acuña shows that these zooplankton use physiologically inert gelatinous bodies to reduce the amount of their tissue that is metabolically active, whilst simultaneously

retaining the physically large bodies needed to house their filtration apparatus. His calculations suggest that a scaled-down salp with the same amount of body carbon, but normal water content (i.e. not gelatinous), would starve to death in a large fraction of the oceans. It thus seems likely that pelagic tunicates use large, gelatinous, but relatively inert bodies to make filter feeding in the open oceans a practical option. As Acuña suggests, we should view these strange creatures as normal animals with the bodies of giants.

1 Acuña, J.L. (2001) Pelagic tunicates: why gelatinous? *Am. Nat.* 158, 100–107

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