proxies of climatic variation from the same sites inferred from $\delta^{18}\text{O}$ data reveal complex community responses to climatic fluctuations. For example, vegetation at one of Yu's sites (Crawford Lake, Ontario) had begun to shift to spruce forest by ~ 500 years after the Bølling–Allerød warming phase ($\sim 12\,700$ years Bp). However, there was a rapid increase in herb pollen percentages at the onset of the Younger Dryas event that was indicative of differential responses among the arboreal and herbaceous components. With the onset of rapid warming at the termination of the Younger Dryas event, however, there is a dramatic change in vegetation that is evident from Yu's data: spruce-dominated forests shifted to pine-dominated forests within a span of ~ 100 years or less, spurred by the onset of Holocene warming.

Such variability in the rate and nature of vegetation responses to climatic events might reflect the importance of factors such as baseline climatic conditions at various sites, biological inertia in the process of succession, facilitation of invasion by some species through the earlier presence of nitrogen fixers, and the proximity of refugia from which species can migrate to recently exposed sites. This last factor might be of particular relevance to Yu's results for post-glacial expansion of spruce, because independent plant macrofossil data indicate that spruce occurred at the very edge of the ice sheet during the Last Glacial Maximum, $\sim 18\,000 \pm 1500$ years Bp [14], and spruce migration rates have been estimated to vary between 0.05 and $>1\text{ km y}^{-1}$, with a median rate of 0.10 km y^{-1} [15,16].

The importance of these two studies lies in their ability to put a finger on just how quickly plant communities appear to have responded, and might continue to respond, to climate change. The beauty of the approaches taken by Williams *et al.* [4] and Yu [5] lies in the fact that, not only do they confirm earlier theoretical predictions of the potential rapidity with which plant community composition might respond to abrupt climate changes, but they also complement the many studies of both plant and animal response to climatic events, variability and change that focus on spatial fluxes (e.g. [3]). The information provided by this pair of new papers, and the others that they will no doubt spawn, will prove valuable in future efforts to model the responses of plant and animal species to predicted climate change. In particular, the quantitative insights provided by these papers might facilitate the mechanistic modeling of climate change-related geographical range shifts and community

dynamics at higher trophic levels, including large herbivores that survived the Pleistocene–Holocene transition [11].

Acknowledgements

I would like to thank David Post, Jack Williams and two anonymous referees for helpful comments and discussions that greatly improved this article.

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doi:10.1016/j.tree.2003.08.008

Letters

Controlling the false discovery rate in ecological research

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A controversial question when analyzing outcomes of ecological research has been whether the increase of type I

error under repeated testing should be taken into account for evaluating the scientific soundness of the results [1–3]. The traditional strong control of the familywise error rate (FWER) (i.e. the probability of obtaining one or more

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spurious rejections) at the 5% level becomes prohibitive in studies involving dozens (or hundreds) of repeated tests. As the research becomes more detailed – and the possibility of getting a higher number of variables increases – the problem intensifies, arriving at the apparent paradox that the more detailed the research, the less the probability of obtaining any significant result [3].

The false discovery rate

Benjamini and Hochberg [4] realized that, in studies where a large number of repeated tests are performed, the researcher might be more interested in controlling the proportion of ‘false discoveries’ (i.e. the proportion of erroneously rejected null hypotheses) than in the probability of obtaining even one spurious rejection. Because controlling false discovery rate (FDR) allows for increased power in large series of repeated tests, this procedure is rapidly becoming established in many areas where studies involving many repeated tests are frequently performed [5,9,10]. Furthermore, the original FDR approach has been the object of successive improvements in recent years [5–8].

Because controlling FDR means a compromise between the application of a well founded statistical principle (alpha-inflation under repeated tests) and the need to avoid the unacceptable loss of power implied by strong control of the FWER in large test tables, it might be a solution for many ecological studies involving highly repeated testing on the same sampling units (as in monitoring), simultaneous tests on many biological or environmental variables, or the re-analysis of many published data sets.

Although most general-purpose statistical programs do

not yet include routines for controlling FDR, several authors involved in FDR findings offer public-domain software on their web sites (http://www.math.tau.ac.il/~roee/FDR_Downloads2.htm; <http://faculty.washington.edu/~jstorey/qvalue/>; <http://www.sph.umich.edu/~nichols/FDR/index.html>).

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doi:10.1016/j.tree.2003.08.011

Phenotypic flexibility

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In a recent paper in *TREE*, Piersma and Drent [1] argue that phenotypic plasticity is a significant factor in understanding animal adaptation. We agree with this thesis and their call for more ‘appropriate phenotypic experimentation, comparison and integration’. We wish, however, to correct their use of our study [2] of the changes in the sizes of the feeding organs of the oyster *Crassostrea gigas*.

In interpreting our observations on seasonal variability in the feeding organs of the oyster (*viz.* the gill:palp ratio), Piersma and Drent superimposed on our data (see their Figure 2) ‘an algal bloom period’ to suggest that the morphological changes are ‘driven by changes in food availability’. Although not cited, these data for an ‘algal bloom period’ were taken from a different study [3] of the continental shelf off the New South Wales (NSW) coast of Australia. Our experiments were done within the Port

Stephens estuary, NSW. Seasonal changes in phytoplankton production off shore are unlikely to determine the food environment for oysters within this estuary.

Independently of the Honkoop *et al.* study, we have measured the particulate food available to the oysters within the Port Stephens estuary [4]. The relationship between food and changes in the feeding organs is complex. In general, an increase in the gill:palp ratio between October and March coincides with a decline in dietary quality (i.e. the organic content of the food particles), rather than an increase in dietary quantity. Later in the year, a decline in food quantity might contribute to a reduction in the gill:palp ratio. Such relationships are consistent with the mechanics of feeding in oysters [5,6] (Figure 1).

Any link between changes in the relative sizes of gills and palps in oysters and seasonal changes in their food environment remains to be formally tested. We believe, nevertheless, that such a study is likely to support the basic

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