

## The stability of forest biodiversity

**T**he unified neutral theory of biodiversity and biogeography<sup>1</sup> provides a dynamic null hypothesis for the assembly of natural communities. It is also useful for understanding the influence of speciation, extinction, dispersal and ecological drift on patterns of relative species abundance, species-area relationships and phylogeny. Clark and McLachlan<sup>2</sup> argue that neutral drift is inconsistent with the palaeorecord of stability in fossil pollen assemblages of the Holocene forests of southern Canada. We show here that their analysis is based on a partial misunderstanding of neutral theory and that their data alone cannot unambiguously test its validity.

Neutral theory in ecology<sup>1</sup> builds on the theory of island biogeography<sup>3</sup>, which asserts that an island or a local community approaches steady-state species richness where there is an equilibrium between the immigration of species from the much larger metacommunity source area and the local extinction of species. The dynamics of a local population are governed by birth, death and immigration events in both neutral and non-neutral models. Under neutrality, at large spatial and temporal scales, Fisher's log-series distribution is the expected steady-state distribution of relative species abundance at the speciation-extinction equilibrium in the metacommunity when the per capita birth and death rates are density independent and the same for all species, and speciation is introduced<sup>4</sup>.

The characteristic timescale for speciation and evolutionary changes in species is much longer than the 200-generation period studied by Clark and McLachlan. During this relatively short time interval, the large-scale metacommunity distribution of relative species abundance, particularly of common and widespread species, will change slowly or remain nearly constant<sup>1</sup>.

Clark and McLachlan's analysis<sup>2</sup> of the fossil pollen record of the eight local tree communities assumes that the sites are undergoing drift in complete dynamic isolation. However, in common with the theory of island biogeography<sup>3</sup>, the neutral theory<sup>1,4</sup> takes into account the fact that the species composition and the dynamics of local communities will be influenced by immigration from the surrounding metacommunity. When the local community is coupled dynamically to the metacommunity, local communities will covary positively in species composition, and exhibit potentially greater compositional stability than if they drifted in complete isolation, as in Clark and McLachlan's simulations.

Dispersal tends to stabilize local species composition and relative abundances because communities become dynamically coupled to one another. Immigrants belonging to the more abundant metacommunity species will arrive more frequently in the local community than immigrants of rarer species, stabilizing local assemblages and making them more similar. Very fast rates of long-distance dispersal may characterize the northward movements of several tree species following the retreat of the continental ice sheets during the Holocene of Europe<sup>5</sup> and North America<sup>6</sup>.

One question is how stable the metacommunity surrounding these local communities has been over the past 10,000 years (the length of the fossil record considered by Clark and McLachlan<sup>2</sup>). Large changes were occurring over this time in the post-glacial forests of eastern North America. Whether or not the metacommunity provided a relatively stable backdrop for the dynamics within the sampled local communities is unclear. However, even if the metacommunity was not perfectly constant or was changing gradually and directionally, abundant metacommunity species would be expected to be major components of virtually all local communities, even communities weakly coupled to the metacommunity with relatively slow or infrequent immigration<sup>1</sup>. A stronger argument for stability inconsistent with neutrality would be to show that local communities persisted in their compositions, despite large changes in the abundances of common species in the metacommunity in which they were embedded.

Figure 1 of Clark and McLachlan<sup>2</sup> is based on simulations of neutral dynamics using a lottery model, which the authors claim measures the divergence among sites, over time, that is expected under neutrality and which should continue to increase until diversity is lost through extinction. But we dispute this. In their model, which does not allow for extinction, the variance actually levels off with time, reaching an equilibrium. Thus, they overestimate the accumulation of among-site variance under neutrality.

Moreover, the timescale for equilibration in Clark and McLachlan's simulations is very different from the evolutionary timescales associated with equilibration of biodiversity in the metacommunity. Biodiversity is maintained in equilibrium in neutral theory because of the balance between speciation and extinction of species on very large spatial and temporal scales. The simplified lottery model used as a neutral benchmark by Clark and McLachlan<sup>2</sup> does not capture a fundamental result of unified neutral theory<sup>1</sup>, namely that the fates of all species in the local community differ according to their unequal abundances in the metacommunity.

Clark and McLachlan note that the distributions of many plant species are strongly correlated with climate, hydrology and soil, but such evidence for niche assembly need not preclude a role for demographic stochasticity (ecological drift). But how strong are the deterministic processes structuring ecological communities relative to drift? Although the hypothesis of complete neutrality may often fail (it is, after all, a null hypothesis), we do not agree with Clark and McLachlan's assertion that the strong evidence for stabilizing forces in the palaeorecord<sup>2</sup> is sufficient to reject ecological drift. Because their lottery model prevents extinction and ignores dispersal and the dynamic coupling between local communities and the metacommunity, it cannot be regarded as a definitive test of current neutral theory.

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**Clark and McLachlan reply** — The neutral model says that the relative abundance of a species is as likely to increase as it is to decrease, because species are ecologically identical<sup>1</sup>. This hypothesis can be rejected if variance does not increase over time<sup>2</sup>. We used a more powerful test, based on comparisons among locations, to show that variability stabilizes and, for most species, decreases over thousands of years<sup>3</sup>. The neutral model also predicts that after a perturbation, relative abundance is as likely to increase as it is to decrease.

Eastern hemlock, a species decimated throughout its range in the mid-Holocene, subsequently increased throughout eastern North America. It did not return to the same densities; it was not expected to because Holocene climates have varied. But the increase from low abundance throughout its range is inconsistent with neutral drift.

Volkov *et al.* object to our analysis, saying that dispersal causes "immigrants belonging to the more abundant metacommunity species to arrive in the local community

more frequently than immigrants of rarer species, stabilizing local assemblages". Their argument says that local populations are maintained by propagule pressure. An abundant species might increase owing to overwhelming seed supply, despite having no competitive advantage. This explanation requires abundant seed emanating from large residual populations. Of course, hemlock was not eradicated from North America. Yet there is no indication of a more abundant metacommunity that could have caused hemlock seeds to arrive more frequently in the local community than did other species. Other species were not rare — the region remained forested throughout. If there was an as yet undiscovered large hemlock population at the time, dispersal data do not support the view that the recovery came from hemlock seed that was sufficiently abundant to overwhelm other species throughout eastern North America. Only beneath hemlock crowns does its seed arrive more frequently than that of other species<sup>4,5</sup>.

One explanation that is consistent with our results, field studies and models is that hemlock competes well in shaded understoreys. An increase from low density is expected in view of its shade tolerance. Differences among species contribute to patterns of diversity across gradients, during succession and with climate change. The predictability of succession, based in large part on shade tolerance, is an example of non-neutral dynamics.

Empirical data and models do not support the view of Volkov *et al.* that dispersal causes tree populations to covary over broad regions (ours exceeds 10<sup>5</sup> km<sup>2</sup>). Seed produced in distant populations makes a small contribution to local density. For this reason, spatial population models predict correlation lengths close to mean dispersal distances (tens of metres)<sup>6,7</sup> and inconsequential representation of lineages that might derive from distant dispersal<sup>8,9</sup>. The latter prediction is consistent with genetic haplotypes<sup>10</sup>. The tight geographic coupling described by Volkov *et al.* could indeed be an outcome of Hubbell's non-spatial model, which assumes global migration of recruits that are immediately everywhere. Unlike dispersal, this assumption is not spatial.

Volkov *et al.* believe that a period of several hundred generations is not long enough to test the unified neutral theory. We stressed that our analysis is not a test of whether speciation offsets extinction; we only tested neutral dynamics<sup>3</sup>.

We agree that our model is not strictly neutral<sup>3</sup>. The lottery example was not used to 'test' for neutrality. We did not dwell on asymptotic behaviour of the model (eventually involving extinction), because it is not relevant for this example — these species co-exist. Species could be assigned identical parameters in any model. The

model simply illustrates how variances increase for identical species, a model-independent prediction. Our test was based solely on observed data.

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#### COMMUNICATIONS ARISING

##### Ecology

## Living in synchrony on Greenland coasts?

Theory indicates that correlated weather may synchronize populations<sup>1</sup>, but the extent to which this holds for non-identical, nonlinear systems is uncertain. Post and Forchhammer<sup>2</sup> claim to have shown climate-induced synchrony for musk oxen and caribou that are separated by the Greenland ice sheet. However, logical and mathematical errors undermine their finding. Whether or not large-scale weather can be a major synchronizing factor across species remains an open question.

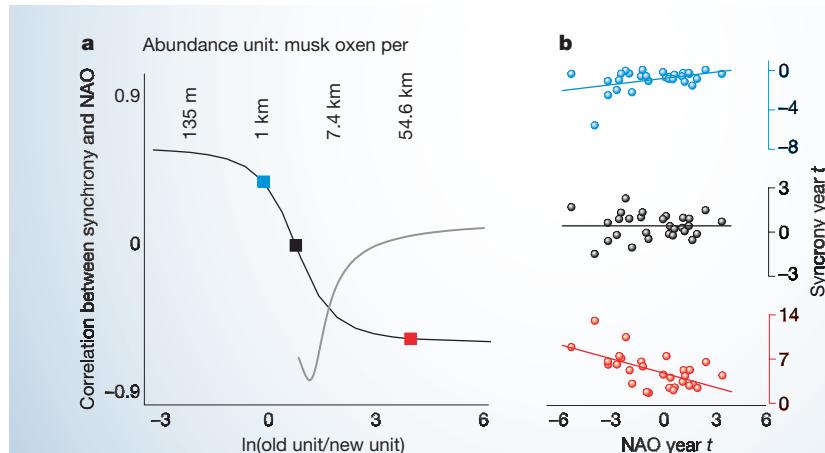
Some caribou–musk-ox population pairs show correlated abundances, and Post

and Forchhammer ascribe this to a high 'North Atlantic Oscillation (NAO) effect ratio',  $\omega_{\text{musk ox}}^{(i)} / \omega_{\text{caribou}}^{(j)}$  where  $\omega_{\text{musk ox}}^{(i)}$  and  $\omega_{\text{caribou}}^{(j)}$  are regression coefficients quantifying how the NAO (ref. 3) affected the growth of each population<sup>4</sup>. However, the effect ratio increases if  $\omega_{\text{caribou}}^{(j)}$  decreases, so the authors' conclusion illogically implies that the less the climate affects caribou, the more climate-synchronized they will be with the musk oxen. Instead, it would be expected that strong climate effects on both populations were a necessary (although not sufficient) requirement for climate-induced synchrony between non-identical systems where local, uncorrelated noise dilutes the effect of shared climatic forcing.

Post and Forchhammer argue that cold winters synchronize population dynamics, reporting a correlation between the NAO and the 'yearly synchrony' (a measure of variability in abundance among populations) within a species. However, synchrony (that is, togetherness in time) requires a temporal aspect, comparing either the timing of events or rates of change, both of which require the availability of more than one time point. The authors' attempt to deduce synchrony from a snapshot of abundances at a single point in time, which is not possible.

Post and Forchhammer's chosen measure of population-size variability is mathematically not well defined, so the results can be turned either way simply by a change of measurement unit (Fig. 1). They calculated the ratio of the mean to the standard deviation of log-transformed abundances,  $\text{sync}(N) = [\text{mean}_{\text{all } i} (\ln N_i) / \text{stdev}_{\text{all } i} (\ln N_i)]$ , for a group of populations in a given year.

However, the mean and standard deviation cannot be compared when using log-transformed data, because the mean of the transformed values depends on the measurement unit used for the raw data, whereas



**Figure 1** Post and Forchhammer's results can be turned either way by a change of measurement unit. **a**, Effect of the choice of unit of measurement on the correlation between NAO and 'yearly synchrony' of musk-ox populations. Squares correspond to scatterplots in **b** (blue, based on raw data; red, Post and Forchhammer's calculations; black, a measurement unit that eliminates the correlation altogether). Post and Forchhammer's adjustment of the unit so that all log-values are positive does not make their synchrony measure well defined, as highlighted by a subset of the data in grey. **b**, Scatterplots against NAO of 'yearly synchrony', using units indicated by the squares in **a**.