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Authors
Hawkins, Bradford A.
Porter, E E

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RESEARCH PAPER

Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America

BRADFORD A. HAWKINS* and ERIC E. PORTER†

*Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697, USA. E-mail: bhawkins@uci.edu; †United States Fish and Wildlife Service, 6010 Hidden Valley Road, Carlsbad, CA 92009, USA. E-mail: eric_porter@fws.gov

ABSTRACT

Aim To investigate the relative contributions of current vs. historical factors in explaining broad-scale diversity gradients using a combination of contemporary factors and a quantitative estimate of the temporal accessibility of areas for recolonization created by glacial retreat following the most recent Ice Age.

Location The part of the Nearctic region of North America that was covered by ice sheets during the glacial maximum 20 000 BP.

Methods We used range maps to estimate the species richness of mammals and terrestrial birds in 48 400 km² cells. Current conditions in each cell were quantified using seven climatic and topographical variables. Historical conditions were estimated using the number of years before present when an area became exposed as the ice sheets retreated during the post-Pleistocene climate warming. We attempted to tease apart contemporary and historical effects using multiple regression, partial regression and spatial autocorrelation analysis.

Results A measure of current energy inputs, potential evapotranspiration, explained 76–82% of the variance in species richness, but time since deglaciation explained an additional 8–13% of the variance, primarily due to effects operating at large spatial scales. Because of spatial covariation between the historical climates influencing the melting of the ice sheet and current climates, it was not possible to partition their effects fully, but of the independent effects that could be identified, current climate explained two to seven times more variance in richness patterns than age.

Main Conclusions Factors acting in the present appear to have the strongest influence on the diversity gradient, but an historical signal persisting at least 13 000 years is still detectable. This has implications for modelling changes in diversity patterns in response to future global warming.

Key words Birds, climate change, diversity gradient, global warming, Ice Age, mammals, recolonization, spatial autocorrelation, species richness.

INTRODUCTION

The influence of present-day climate on broad-scale patterns of species richness is firmly established (Wright *et al.*, 1993; Hawkins *et al.* in press a). However, the extent to which historical conditions also explain patterns is less well documented and represents a contentious issue (e.g. Currie & Paquin, 1987; Latham & Ricklefs, 1993; McGlone, 1996; Francis & Currie, 1998; Currie, 2001). It is well known that species ranges have shifted in North America following post-Pleistocene climatic warming (Pielou, 1991; Graham *et al.*, 1996), and analyses of diversity gradients on this continent have found that variables reflecting present conditions are able to explain most of the variation in species richness (Currie, 1991; Danell *et al.*, 1996; Badgley & Fox, 2000). Workers do not dismiss the possibility that longer-term effects may also be operating, but identifying such effects has been hampered by an inability to generate quantitative measures of historical events. Danell *et al.* (1996) in particular summed up the nature of the problem when they concluded in their analysis of boreal mammal diversity that, 'our study shows that present-day conditions such as productivity and species-area relationships may play important roles in determining community composition of mammal herbivores at a large

Correspondence: Bradford A. Hawkins, Department of Ecology & Evolutionary Biology, University of California, Irvine, CA 92697, USA. E-mail: bhawkins@uci.edu

spatial scale. This is not to say that, e.g. glacial history is unimportant. However, we have found it difficult to include such historical events in a quantitative and sensible way into our analyses'.

In this paper we address the issue of how historical and current factors may act in concert to explain diversity patterns in northern latitudes, focusing on the part of North America in which it is possible to generate a quantitative variable describing the glacial history of the region encompassing events occurring over the past 20 000 years. Our goals are to evaluate simultaneously the explanatory power of present climates and the most recent Ice Age for the diversity gradient for mammals and birds, and to attempt to reconcile points of view that focus exclusively on current vs. historical processes as they influence broad-scale diversity patterns, at least for this part of the world. Due to the relatively short time period over which we test for a historical signal, we do not consider how richness patterns may originate due to differences in diversification rates in different regions (see e.g. Cardillo, 1999); rather we focus on how species that already exist rearrange themselves geographically in response to prolonged climate change. Thus, we contrast current influences with those arising from geologically 'short-term' historical events.

METHODS

We generated eight potential explanatory variables for the diversity pattern of mammals and terrestrial birds in northern North America. Seven of the variables describe factors operating primarily at present and comprise a set of variables that have been used in other analyses of diversity gradients in the Nearctic (e.g. Currie, 1991; Kerr & Packer, 1997, 1999; Badgley & Fox, 2000; Hawkins *et al*. in press b). The variables (and sources) were: annual potential evapotranspiration (Priestley-Taylor formula) (http://www.grid.unep.ch/data/grid/gnv183.php), annual actual evapotranspiration (Thornthwaite's) (http://www.grid.unep.ch/data/grid/gnv183.php), range in elevation (derived from a combination of spot heights and contour lines in the topographical maps in The Pergamon World Atlas (1968), estimated to the nearest 50 m), mean monthly temperature (http://www.grid.unep.ch/data/grid/gnv15.php), mean January temperature (from http://www.grid.unep.ch/data/grid/gnv15.php), annual precipitation (http://www.grid.unep.ch/data/grid/gnv174.php) and landcover diversity (the number of landcover types calculated from 8 km resolution AHVRR data, NOAA pathfinder land [PAL] program) (http://www.geog.umd.edu/landcover/8 km-map.html).

The eighth variable represents the historical events associated with the most recent Ice Age and was also used to delimit the geographical scope of the study (Fig. 1). We used the temporal series of maps generated by Dyke & Prest (1987), supplemented with maps at http://members.cox.net/quaternary/nercNORTHAMERICA.html, showing the extent of ice

Fig. 1 The maximum extent of glaciation during the most recent Ice Age (*c*. 20 000–6000 years before present). Also shown are the general pattern of glacial retreat up to *c*. 6000 BP and the last area remaining under ice in north-eastern Quebec prior to the complete melting of the ice sheet from the main continent between 7000 and 6000 BP. Parts of Alaska, although also glaciated, were excluded because we were uncertain of the detailed pattern of glacial retreat. Based on Dyke & Prest (1987).

covering continental North America during the most recent Ice Age, to estimate the time when land became exposed as the ice retreated and glacial lakes drained. The area completely covered by ice during the glacial maximum was divided into 164 equal-area cells of 220 × 220 km each (adjacent coastal cells were often combined to keep total land area in each cell as constant as possible; islands were excluded). In each cell we estimated values for the current factors as well as the number of years before present when at least part of the cell became exposed for potential colonization by terrestrial organisms, as indicated by the change in ice/water cover from one mapped time period to the next. These potential explanatory variables were then analysed with respect to the number of native mammal and birds species occupying each cell, based on the range maps in Hall & Kelson (1959) and the National Geographic Society (1999). For the birds, aquatic and marine species were excluded.

We first determined which variables were most strongly associated with species richness using multiple regression. Because of spatial autocorrelation in the data, the probabilities associated with these analyses are too liberal, but the focus of our analysis was on the ability of variables to explain the variance in mammal and bird richness rather than on fixing significance levels (although we did use the standard 0.05
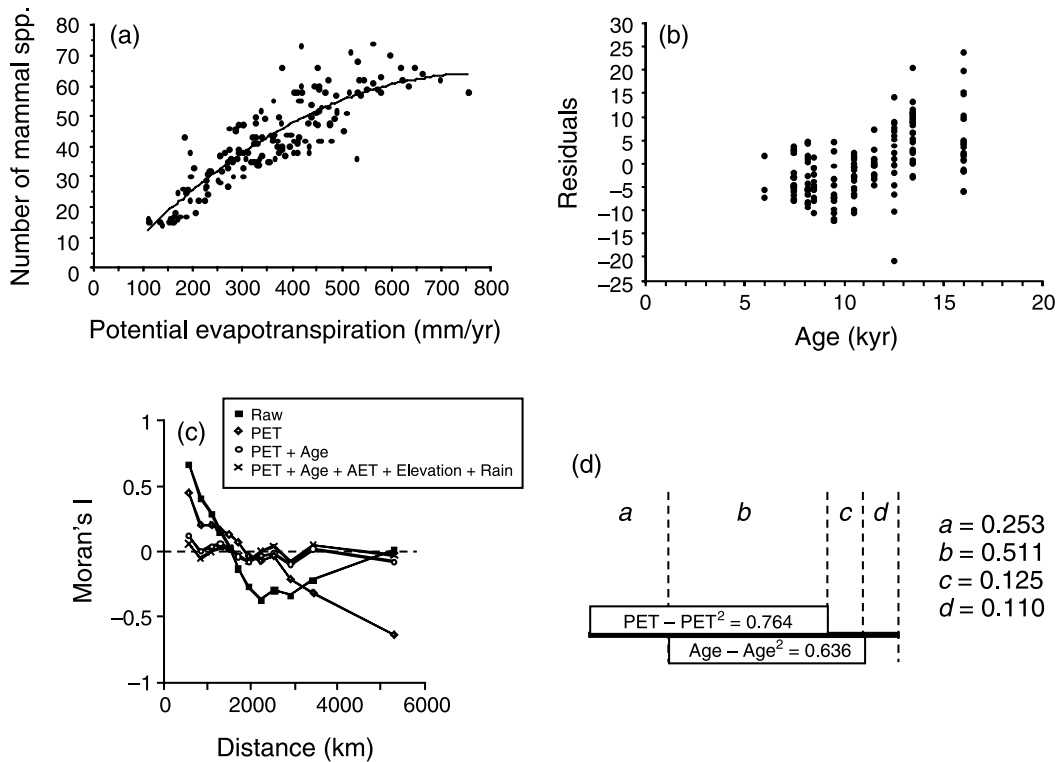
Fig. 2 The relationships between (a) current energy inputs (potential evapotranspiration) and mammal species richness using a quadratic fit and (b) years since exposure from glacial ice/lakes and residual variation remaining after fitting PET (see Table 1a for statistics). (c) Correlograms of Moran's I showing patterns of spatial autocorrelation of raw mammal richness and residual autocorrelation after sequentially adding PET, cell age and minor variables to multiple regression models. (d) Partial regression partitioning the independent contributions of PET, a, and cell age, c, and the overlap between them, b, on coefficients of determination for mammal richness. d represents the proportion of variation in richness not explained by either factor.

significance level to include variables in the models). Further, examination of the residuals in species richness after fitting the environmental variables indicated that our models account for most of the spatial pattern in richness, so the influence of spatial autocorrelation on the significance levels in the regressions is very slight. We also used a spatial analysis to evaluate how well each predictor variable explains the pattern of mammalian and avian richness across a range of spatial scales (see Diniz-Filho *et al.*, 2003). We first calculated Moran's I (a widely used autocorrelation coefficient) across 12 distance classes for the raw species richness data, using SAAP 4.3 (Wartenberg, 1989), followed by sequentially generating correlograms on residual richness after fitting each predictor variable. Reduction in the level of spatial autocorrelation in any distance class after fitting each predictor variable represents the ability of that variable to explain richness at that distance. No reduction, or an increase, in spatial autocorrelation at any distance indicates that the fitted variable is a poor predictor of richness at that distance. Any autocorrelation remaining in any distance class after fitting all predictor variables indicates

that some of the variance not explained by the regression model contains spatial structure.

Because we expect past climates to be spatially correlated with present climates across northern North America, and the pattern of glacial retreat must be associated with past climatic conditions, we also conducted partial regression analyses (Legendre, 1993; Legendre & Legendre, 1998) to partition the variance explained by contemporary vs. historical effects. The coefficients of determination for current climate and cell age separately were obtained from simple regression models, which in all cases were best described as second-order polynomials with negative squared terms (see Figs 2d and 3d). The coefficients of determination for climate and age combined were obtained from the multiple regressions (in which age was best described by different variable structures than in the simple regressions, see Table 1). The three coefficients of determination can then be used to partition the independent effects of contemporary climate, cell age, and the overlap between them.

A final consideration is that the analysis might be considered 'biased' by the inclusion of many contemporary variables but
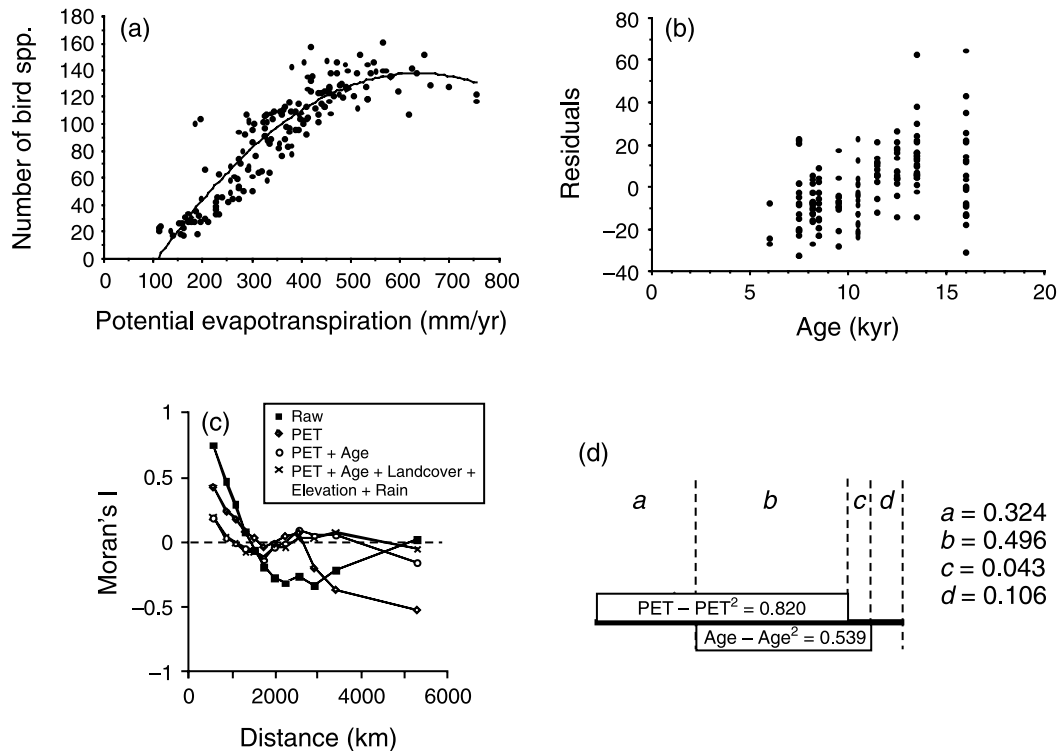
Fig. 3 The relationships between (a) current energy inputs (potential evapotranspiration) and bird species richness using a quadratic fit and (b) years since exposure from glacial ice/lakes and residual variation remaining after fitting PET (see Table 1b for statistics). (c) Correlograms of Moran's I showing patterns of spatial autocorrelation of raw bird richness and residual autocorrelation after sequentially adding PET, cell age and minor variables to multiple regression models. (d) Partial regression partitioning the independent contributions of PET, *a*, and cell age, *c*, and the overlap between them, *b*, on coefficients of determination for bird richness. *d* represents the proportion of variation in richness not explained by either factor.

Table 1 Step-forward multiple regression models for species richness patterns of mammals and terrestrial birds in northern North America. Squared terms were added when significant, and the probabilities associated with the linear and squared terms are shown separately. Probabilities associated with individual predictor variables are slightly biased due to the presence of some residual spatial autocorrelation in the data not accounted for by the models (see Figs 2 and 3)

Variable	Cumulative R^2	Probability linear	Probability squared
A. Mammals			
PET – PET^2	0.764	< 0.0001	< 0.0001
Age + Age^2	0.901	< 0.0001	0.002
Range in elevation	0.905	0.012	
Precipitation	0.917	< 0.0001	
B. Birds			
PET – PET^2	0.820	< 0.0001	< 0.0001
Age	0.898	< 0.0001	
Landcover diversity	0.905	< 0.0001	
Range in elevation	0.909	0.014	
Precipitation	0.913	0.007	

only one historical variable. However, it should be remembered that the variables we included were not a random sample of all possible explanatory variables but were selected based on previous analyses of broad-scale richness gradients in this region, which have primarily focused on contemporary effects (Currie & Paquin, 1987; Currie, 1991; Danell *et al*., 1996; Kerr *et al*., 1998, 2001; Kerr & Packer, 1999; Badgley & Fox, 2000; Kerr, 2001; Hawkins *et al*. in press b). Our goal is not to test whether contemporary climate is statistically associated with richness gradients in the northern Nearctic; it is already very well documented that it is. Rather, we ask if incorporating a historical variable contributes anything to a statistical explanation of the contemporary richness gradient beyond (or instead of) that provided by measures of current conditions.

RESULTS

Mammals

The multiple regression model for mammals identified potential evapotranspiration (PET) as the strongest predictor of species richness, explaining 76% of the variance (Table 1a).

As is often found in analyses of animal diversity gradients in northern latitudes, the relationship was curvilinear, with richness being strongly associated with PET at PET levels below *c.* 550 mm/year, but less so above that level (Fig. 2a). The second strongest variable was the age of the cell, which explained an additional 13.7% of the variance. A plot of residual richness (after fitting PET) against cell age gave a visual impression of a possible third-order polynomial relationship (Fig. 2b). However, although a second-order polynomial age model was significantly better fitting than a linear model in the multiple regression (Table 1a), a cubic term was marginal ($P = 0.042$) and increased the multiple coefficient of determination by only 0.007, and thus was excluded from the final model. Two additional factors also entered the regression model, but their contributions to the explained variance were very small.

Comparisons of the correlograms after fitting each predictor variable also identified both PET and cell age as important descriptors of the mammal richness gradient (Fig. 2c). Raw richness showed strong positive spatial autocorrelation at distances less than 1300 km, with negative autocorrelations at intermediate distances, and no autocorrelation at the largest distance class (i.e. at the eastern and western ends of the region). Fitting PET moderately reduced the spatial autocorrelation at small distances, and strongly reduced the autocorrelation at intermediate distances, but actually increased autocorrelation at the largest distances (residual richness is high in the west and low in the east). This indicates that PET provides a partial explanation for the spatial pattern of mammal richness at shorter distances (< 1300 km), a strong explanation at distances between 1500 and 2500 km, but a very poor explanation at distances greater than 2900 km (i.e. along the east to west continental axis). However, fitting cell age removed most of the remaining autocorrelation across all distances (Fig. 2c), indicating that this variable is required to explain most of the spatial pattern at both short and large distances. Fitting range in elevation and annual precipitation further removed small amounts of the remaining residual spatial autocorrelation, although significant, albeit low, levels of autocorrelation remained at the first and tenth distances classes. Even so, the spatial analysis reinforces the result of the multiple regression that elements of both present climate and the age/palaeoclimate of areas appear to operate in concert to explain the contemporary diversity gradient.

As expected, covariation between contemporary PET and cell age makes it impossible to distinguish fully their contributions to the diversity gradient, and half of the variance is explained by the overlap between these variables (Fig. 2d). Of the portion of the variance to which independent effects could be attributed, current climate accounted for twice as much variance as cell age. Thus, as in the multiple regression, PET is identified as having the strongest independent influence on diversity, with age being secondary. However, half of the variance in richness cannot be attributed to either factor unambiguously, indicating that an alternative approach is necessary to disentangle fully current and historical effects.

Birds

The results for bird diversity were qualitatively identical to those found for mammals. The multiple regression identified PET as the strongest predictor of richness (Table 1b), with a curvilinear relationship (Fig. 3a). Age further improved the model by 8% and was positively linearly associated with residual species richness (Fig. 3b) (a squared term was not significant in the multiple regression ($P = 0.305$)). Three additional variables also contributed to the regression model, but their explanatory power was trivial (Table 1b). The pattern of spatial autocorrelation in raw species richness was similar to that of mammals (Fig. 3c). The spatial pattern in residual richness after fitting PET was also very similar; PET partially explained the pattern at small distances, explained the pattern well at intermediate distances, but explained the pattern poorly at large distances. Fitting cell age removed most of the autocorrelation at both small and large distances, and fitting the three minor variables further reduced large-scale autocorrelation. As with mammals, low amounts of residual autocorrelation remained in some distance classes, indicating that additional spatially patterned variables not included in the analysis are probably contributing slightly to the diversity gradient.

Approximately half of the variance in bird richness was explained by the overlap between contemporary PET levels and cell age (Fig. 3d). However, in contrast to mammals, where the independent contributions of PET and age were somewhat balanced, for birds most of the variance that could be independently attributed to the two factors was due to PET, with only a small independent contribution by cell age.

DISCUSSION

Our analysis is consistent with the idea that present energy inputs, as measured by annual potential evapotranspiration, explain the most variance in the geographical pattern of species richness of mammals and birds in the northern Nearctic. The overriding importance of energy is congruent with previous studies focused on vertebrates in the far northern latitudes (Terent'ev, 1963; Heggberget, 1987; Currie, 1991; Lennon *et al.*, 2000; Hawkins *et al.* in press b). However, we also find that the historical pattern of retreat of the ice sheets in response to post-Pleistocene global warming has left a signal on bird and mammal richness still detectable after at least 13 000 years. Although we cannot be certain that cell age in fact represents a purely historical variable, the analysis indicates that polarized arguments that only current or only historical processes influence diversity gradients are probably incorrect. On the other hand, based on the amounts of variation explained by PET and cell age, our results are consistent with

the hypothesis that current climate has the strongest influence on diversity, with history playing a secondary role (Whittaker & Field, 2000).

The relative importance of current and historical conditions as predictors of mammal and bird diversity patterns is also consistent with what we would expect based on their relative dispersal abilities, although birds and mammals also differ in other ways that might influence their ability to recolonize newly exposed areas. In general, bird dispersal rates should be greater than for mammals, so we would expect the former to be able to respond to climate change more rapidly. As indicated by the partial regression (see Figs 2d and 3d), the historical signal is indeed much stronger for mammals than for birds relative to the signal arising from PET, although the covariation between cell age and contemporary energy levels makes it impossible to disentangle fully their effects. Given the well known migratory habits of many bird species in Canada, it is perhaps surprising that any historical signal can be detected at all.

An obvious question this analysis raises is if similar results might be found in the Palearctic, which was also extensively glaciated during the Pleistocene. However, two lines of evidence suggest that our result is unique to the Nearctic, at least for mammals and birds. First, Palearctic animals have had more time to recolonize even the youngest parts of Eurasia compared to North America. The ice sheet had disappeared from continental Eurasia more than 9000 years ago (Adams & Faure, 1997), whereas it persisted in north-eastern Canada until *c.* 6000 years ago (Dyke & Prest, 1987). Second, the ice sheets were much more extensive in the Nearctic than in the Palearctic. For example, the minimum distance between the edge of the ice sheet at glacial maximum to the most recently exposed land in North America (i.e. from western New York to north-west of Lac Caniapiscau in north-east Quebec, see Fig. 1) is *c.* 1600 km, whereas in Eurasia the minimum distance (from Rubinskoye Vodokhranilishche in north-western Russia to south-west of Inarijarvi in northern Finland) is *c.* 900 km. Thus, Eurasian organisms have generally had to cover less distance to recolonize all of the land that was glaciated and have had more time to do it. For these reasons we doubt that a strong historical signal on bird and mammal richness arising from the most recent Ice Age remains in the Palearctic, although it might still be detectable in groups with more limited dispersal abilities (but see Williams *et al.*, 2002). A comparative analysis of Nearctic and Palearctic trees would answer this question.

Although this study was not focused on documenting the effect of global climate change on diversity patterns, the results are relevant to this issue. If species are able to adjust their ranges in response to global warming very quickly (see, e.g. Parmesan *et al.*, 1999), then we would expect the effect of climate change to be quickly masked by postchange dispersal. However, we find what appears to be a lag in the recolonization of Canada even after areas have been exposed for at least 13 000 years (see Figs 2b and 3b), and in some areas the effects remain relatively strong. For example, our PET-based climate model predicts that the youngest cells in Canada should support 31.4 mammals/cell and 62 birds/cell, whereas observed diversities are 23.4 mammals and 42.3 birds per cell. Thus, a diversity model based on present energy levels alone overestimates richness in these cells by 21–25%.

In sum, we find that although current climate represents a strong predictor of mammal and bird diversity gradients in the northern Nearctic, historical conditions may have a role to play. The northern Nearctic represents an unusual case where the pattern of glacial retreat allows us to generate a quantitative measure of gradual climatic warming extending almost 14 000 years by providing estimates of when local temperatures had risen to levels sufficient to melt the ice sheets in different parts of North America (we cannot say anything about local conditions after it was warm enough to melt all of the ice, although recolonization of deglaciated areas must have also been further delayed due to polar desert conditions near the ice sheets and lagged recolonization by plants). However, in more southern regions where glaciation did not occur or was not extensive, it will be more challenging to identify proxy variables for historical conditions to use in analyses of diversity patterns. This will be especially difficult for events occurring in much deeper time, but even if we restrict ourselves to effects extending over thousands of years rather than millions of years, it may be that the spread of ice sheets during ice ages represents such an extraordinarily strong event that the effects we find are restricted to the far northern latitudes. Irrespective, climate change appears to have left an imprint on the diversity gradient in Canada, and the history of the region should not be ignored.

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BIOSKETCH

B. A. Hawkins' current research is focused on large-scale patterns in ecology, particularly global diversity gradients. He also maintains an interest in the biology and ecology of insect parasitoids.