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Summer vegetation, deglaciation and the anomalous bird diversity gradient in eastern North America

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ABSTRACT

Aim Geographic variation in the species richness of birds has been shown to be strongly associated with annual water and energy levels (actual evapotranspiration, AET) at the global scale. However, the gradient in eastern North America appears to be anomalous, because richness is greatest around the Great Lakes, whereas AET is highest in the south-eastern US. Here I examine if birds may be responding to vegetation produced during the breeding season rather than to annual production.

Location North America east of longitude 98° W.

Methods The bird richness pattern was examined using climatic variables, remotely sensed estimates of annual and seasonal plant biomass, and time since areas were exposed by the retreating Laurentide ice sheet from 20,000 to 6000 yr BP.

Results Average summer GVI (Global Vegetation Index, derived from NDVI) was found to be positively linearly associated with richness, explaining 82% of the variance, whereas the relationships between richness and annual measures of both AET and GVI were curvilinear. The pattern of retreat of the Laurentide ice sheet explained an additional 6% of the variance in richness, consistent with a previous analysis of Canadian birds.

Main conclusions In eastern North America, a seasonal variable associated with plant production explains the diversity gradient rather than the annual measures, but it does not undermine a general conclusion that bird diversity is closely linked with plant biomass. Further, both contemporary and historical factors appear to influence the gradient, and an association between bird richness and the geographic pattern of glacial retreat is detectable in both climatic and plant-biomass models of bird diversity.

Keywords

Bird species richness, diversity gradients, global vegetation index, ice age, NDVI, palaeoclimates, productivity, spatial autocorrelation.

INTRODUCTION

Hawkins *et al.* (2003) used data for the terrestrial birds of North and South America, Europe, Africa, northern Asia, and Australia to examine broad-scale bird richness gradients and found that a generalized linear model comprising annual actual evapotranspiration (AET) and the identity of the biogeographical region explained 78.4% of the variance in species richness, with AET explaining 72.4% and region 6.0%. Based on this result and the known relationship between AET and plant productivity at the global scale (Rosenzweig, 1968; Lieth, 1975), Hawkins *et al.* (2003) concluded that plant productivity represents the probable explanation for the global bird gradient, but that the historical

signal associated with biogeographical region also had a small but significant influence on the pattern. However, they also noted that the regional effect was largely due to an anomalous diversity gradient in eastern North America, arising because both bird richness and AET increase from subarctic Canada to the Great Lakes region, but bird richness decreases south of the lakes whereas annual AET continues to increase. This humped richness pattern has been known for some time (Cook, 1969) and also exists when only North American endemic species are considered (Hawkins & Diniz-Filho, 2002). Thus, in this region, plant 'productivity' and bird richness appear to be decoupled, and it remains unclear what might drive the bird richness gradient in eastern North America.

Two recent analyses of bird diversity gradients in North America suggest a solution to the conundrum of why breeding bird richness drops south of the Great Lakes. First, Hurlbert & Haskell (2003), focusing on seasonal bird richness patterns in the part of North America covered by the North American Breeding Bird Survey and the Audubon Christmas Bird Count, working at small grain sizes, and using sample data rather than range maps, found noisy but linear positive relationships between seasonal bird diversities and June vs. December NDVI (Normalized Difference Vegetation Index). This estimate of plant standing crop or 'greenness' is derived from remotely sensed AVHRR data and is being used as a proxy for productivity (see Hurlbert & Haskell, 2003), although the actual relationship between 'greenness' and 'productivity' remains unquantified. Further, a map of June NDVI (Hurlbert & Haskell, 2003, Fig. 4b) also suggested that summer biomass in eastern North America may in fact be higher in the Great Lakes areas than in both north-eastern Canada and the south-eastern USA. Second, a large-grained analysis by H-Acevedo & Currie (2003) similarly found linear positive relationships between seasonal bird diversities and NDVI, although they reported that richness was more strongly associated with water and energy variables. Following these authors, summer and annual estimates of plant production derived from the AVHRR data were generated to determine if the North American anomaly might represent a case where production may indeed drive bird diversity, but in contrast to the other geographical regions, measures of seasonal production may describe the relationship rather than measures of annual production.

METHODS

The estimates of plant production were based on the Monthly Generalized Global Vegetation Index (GVI) (Kineman & Hastings, 1992), accessible online at http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_a/datasets/a01/mgv.htm#top. This index is derived from a 1-km resolution NDVI converted by Kineman & Hastings into a 10-minute grid system, composited monthly and rescaled. This coarser resolution was considered more appropriate for the grain size of my grid system (48,400 km²). The monthly data extending from April 1985 to December 1988 (the entire dataset available) were used to generate average monthly GVI across all months (annual GVI) and average monthly GVI for June, July and August only (summer GVI).

The geographical scope of the analysis was 140 sample cells in a grid encompassing all of continental North America east of a line running from McAllen, Texas to the Boothia Peninsula on the northern Canadian coast. This encompasses the part of North America in which the richness gradient appears humped with respect to latitude (see Hawkins *et al.*, 2003, Fig. 3). Values for both vegetation variables within each grid cell were calculated as the average of 10 randomly selected pixels, after excluding points from lakes or oceans. Annual GVI was generated to compare against annual AET to determine if the latter actually represents an accurate estimate of the amount of vegetation in the region averaged over the entire year, and summer GVI was

generated to test if production during the growing season is associated with the species richness of breeding birds, all of which are resident over the summer (whereas migratory species move south for the winter).

A historical variable recently found to be associated with bird richness in northern North America was also incorporated. Hawkins & Porter (2003) examined the diversity gradients for terrestrial birds and mammals in the part of North America that was covered by ice sheets during the most recent Ice Age. They found that annual potential evapotranspiration (PET; a measure of ambient energy inputs) explained 82.0% of the variance in the bird richness gradient, and that the length of time a cell had been exposed since the retreat of glacial ice/lakes explained an additional 7.8% of the variance. They concluded that the glacial history of northern North America had left a small but measurable imprint on the contemporary diversity gradient. To determine if the inclusion of the vegetation index might change that conclusion, and to generate a more complete model of bird richness, cell age was included as a potential explanatory variable. This variable ranges from 6 to 16 k year in the glaciated part of the region (see Hawkins & Porter, 2003). For cells south of the glacial maximum, an arbitrary cell age of 20 k year was assigned.

The analysis comprised first examining the relationships between annual AET, annual GVI, summer GVI, cell age, and bird species richness visually, followed by a step-forward multiple regression to generate a model of richness patterns. Also included in the analysis were annual PET, mean daily January temperature, range in elevation and annual precipitation, as these variables might reasonably be expected to influence bird richness to some extent. After generating the multiple regression model, SAAP 4.3 (Wartenberg, 1989) was used to generate a spatial correlogram of raw species richness at 12 distance classes, followed by correlograms of residual richness generated after each step in the multiple regression. Reduction in spatial autocorrelation at any distance after fitting each variable reflects the ability of that predictor variable to explain the spatial richness pattern. Any spatial autocorrelation remaining after fitting all predictor variables indicates that some of the variance not explained by the model contains spatial structure (Diniz-Filho *et al.*, 2003).

RESULTS

The relationship between bird richness and annual AET in eastern North America was as reported by Hawkins *et al.* (2003) (Fig. 1a). In Canada, AET and richness are strongly positively associated, but south of the Great Lakes the relationship becomes negative. Annual GVI shows a qualitatively similar relationship with bird richness, being positive when both are low and becoming weakly negative in areas of high GVI and richness (Fig. 1b). This similarity of patterns reflects the fact that annual GVI and annual AET are strongly positively correlated ($r = 0.869$, $P < 0.001$). Thus, neither annual measure of plant production can by themselves adequately explain bird richness in eastern North America since they are not linearly associated with diversity throughout the region.

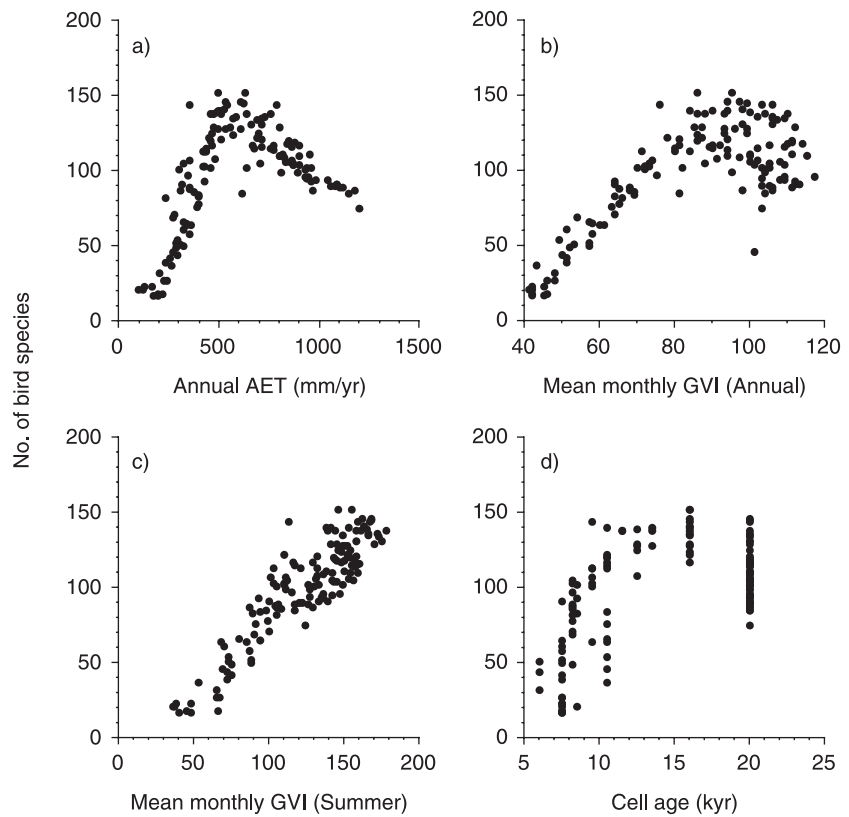


Figure 1 Relationships between bird species richness in eastern North America and: (a) annual actual evapotranspiration (AET) (b) monthly global vegetation index (GVI) averaged over the entire year (c) monthly global vegetation index averaged over June, July and August, and (d) the length of time cells have been available for recolonization as the Laurentide ice sheet retreated during the last ice age (20,000, i.e. 6000 years before present). Cells that were not completely covered by ice were assigned an age of 20,000 years.

Table 1 Multiple regression model of terrestrial bird species richness for eastern North America. Probabilities are biased by the presence of spatial autocorrelation in the richness data

Variable	Cumulative R ²	P-value
Summer GVI	0.822	< 0.001
Age – Age ²	0.878	< 0.001
PET	0.883	< 0.018
Precipitation	0.890	< 0.005

Summer GVI, average monthly global vegetation index for June, July and August; Age, years since deglaciation; PET, annual potential evapotranspiration; Precipitation, annual precipitation.

In contrast to the annual measures, mean monthly GVI during the summer was strongly linearly associated with bird richness everywhere (Fig. 1c), and summer GVI entered the multiple regression model as the strongest predictor, explaining 82% of the variance (Table 1). Cell age had a curvilinear relationship with bird richness (Fig. 1d) and also entered the multiple regression model as a second-order polynomial (Table 1), explaining an additional 5.6% of the variance in richness. PET and annual precipitation then entered the regression model (Table 1) but contributed little to the coefficient of determination.

The spatial pattern of autocorrelation in the raw richness data is characteristic of a unimodal cline (Fig. 2), with strong positive autocorrelation at short distances, gradually becoming negative at intermediate distances and then reversing at long distances.

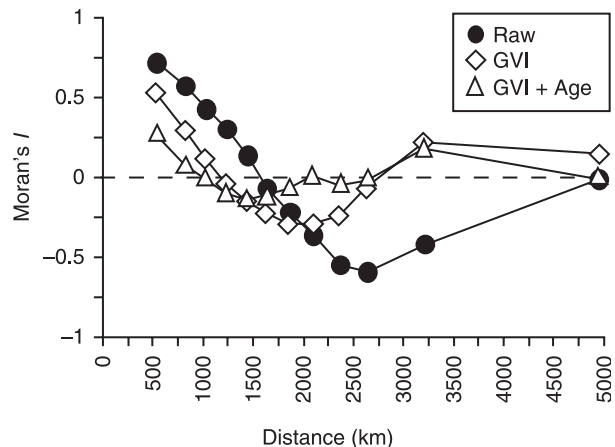


Figure 2 Spatial correlogram across 12 distance classes for raw bird species richness and for residuals after sequentially fitting the three best explanatory variables in the multiple regression model given in Table 1. All correlograms are significant ($P < 0.001$, Bonferroni adjusted), indicating that significant residual spatial autocorrelation remains in at least one distance class.

Although fitting summer GVI removed 42% of the average spatial autocorrelation across all distances, a substantial amount of unexplained spatial pattern remained at 500 km and between 1500 and 2000 km (Fig. 2). The negative autocorrelation at mid-distances also indicates that significant ‘humpedness’ remains in the diversity data after fitting GVI. When cell age entered the model during the step-forward procedure, the

average autocorrelation was further reduced to 25% of the original, whereas adding PET and precipitation slightly increased the average residual autocorrelation (not shown). It is notable that significant autocorrelation remains in several distance classes, indicating that part of the 11% of the unexplained variance in the regression model may eventually be explained by the addition of other as yet unidentified spatially patterned variables operating at local- and meso-scales. From a statistical point of view, it also means that the data points in each cell are not fully independent, and thus the probabilities in the multiple regression are too liberal (see Diniz-Filho *et al.*, 2003 for discussion of this issue). However, even though the model may not explain all of the spatial pattern (after all, the coefficient of determination is not 1.00), it is clear that summer plant production and glacial history in concert describe well the unimodal diversity gradient in the eastern region of North America.

DISCUSSION

This analysis indicates that the failure of the south-eastern United States to conform to the linear relationship found between actual evapotranspiration and bird diversity for the rest of the world (Hawkins *et al.*, 2003) does not seriously undermine the conclusion that plant production represents the primary driving force for bird richness at the global scale. Rather, it suggests that seasonal pulses of production may be critical to birds rather than annual averages of biomass, as reasoned by Hurlbert & Haskell (2003) (see also Lennon *et al.*, 2000; for a related argument with respect to seasonal temperatures). Of course, it could be argued that this is true in all parts of the world, which raises the question of why annual AET explains so much variance in most geographical regions whilst it does not in the south-eastern United States. This will be difficult to answer empirically, because 'seasons' and bird residence times vary in complex patterns in different parts of the world, making a comparison of annual and seasonal models difficult. Irrespective, this does not affect the general explanatory power of plant production.

An important aspect of this analysis and those of Hurlbert & Haskell (2003) and H-Acevedo & Currie (2003) when compared to Hawkins *et al.* (2003) is that the latter study estimated plant production using a climatic proxy, so it was not possible to determine unambiguously whether AET operates on bird richness directly via temperature and/or water stresses on birds or indirectly via potential food availability. The remotely sensed vegetation data in both Hurlbert & Haskell (2003) and this study implicate the importance of vegetation per se. However, H-Acevedo & Currie (2003) reported that climate variables better describe bird diversity than NDVI, so the issue of direct vs. indirect effects of climate is still open to debate.

I also found that the weak but detectable relationship between richness and the spatial pattern of glacial retreat reported by Hawkins & Porter (2003) is robust to the addition of the new plant production variable. The amount of variance explained by

this measure of glacial history is a bit less than found for a PET-based model for the whole of Canada (5.6% vs. 7.8%), but the results are not strictly comparable, since this study includes only the eastern half of the continent as well as areas that were not glaciated at all. Even so, a probable secondary effect of Pleistocene climate on the contemporary bird diversity gradient in the northern Nearctic is observable, irrespective of the specific contemporary model used.

In sum, it appears that the 'anomalous' diversity gradient in eastern North America is not so odd after all, but simply suggests that seasonal measures of plant biomass or productivity sometimes better explain bird richness gradients than annual measures. Even so, given the results of Hawkins *et al.* (2003), Hurlbert & Haskell (2003), H-Acevedo & Currie (2003) and this study, the importance of plant production to maintaining the richness of a diverse group of vertebrates across large geographical extents is becoming increasingly evident.

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BIOSKETCH

B. A. Hawkins' current research is focused on large-scale patterns in ecology, particularly global diversity gradients.