Disparities between observed and predicted impacts of climate change on winter bird assemblages

Frank A. La Sorte*, Tien Ming Lee, Hamish Wilman and Walter Jetz

Ecology, Behavior and Evolution Section, Division of Biological Sciences, University of California, San Diego, 9500 Gilman Drive, MC 0116, La Jolla, CA 92093-0116, USA

Understanding how climate change affects the structure and function of communities is critical for gauging its full impact on biodiversity. To date, community-level changes have been poorly documented, owing, in part, to the paucity of long-term datasets. To circumvent this, the use of 'space-for-time' substitution—the forecasting of temporal trends from spatial climatic gradients—has increasingly been adopted, often with little empirical support. Here we examine changes from 1975 to 2001 in three community attributes (species richness, body mass and occupancy) for 404 assemblages of terrestrial winter avifauna in North America containing a total of 227 species. We examine the accuracy of space-for-time substitution and assess causal associations between community attributes and observed changes in annual temperature using a longitudinal study design. Annual temperature and all three community attributes increased over time. The trends for the three community attributes differed significantly from the spatially derived predictions, although richness showed broad congruence. Correlations with trends in temperature were found with richness and body mass. In the face of rapid climate change, applying space-for-time substitution as a predictive tool could be problematic with communities developing patterns not reflected by spatial ecological associations.

Keywords: avian communities; body-size distributions; climate change; longitudinal analysis; space-for-time substitution; species richness

1. INTRODUCTION

Modern global climate change (Karl & Trenberth 2003) and land-use change (Lambin & Geist 2006) are projected to be the primary drivers for future global change, with significant negative implications for biodiversity (Sala *et al*. 2000; Jetz *et al*. 2007). However, the ecological impact of climate change on biological communities and the long-term implications remain poorly understood. Investigations that have examined or modelled the impact typically focus on the response of individual species (Warren *et al*. 2001; Jetz *et al*. 2007; La Sorte & Thompson 2007). When entire communities are examined, investigations are often geographically confined, resulting in limited inferential scope (Warren *et al*. 2001; Lemoine *et al*. 2007*a*). Overall, these shortcomings have constrained our ability to understand past impacts and predict future consequences for species, communities and ecosystems.

The paucity of long-term datasets has made popular the use of 'space-for-time' substitution in ecological research (Pickett 1987; Dunne *et al*. 2004; Fukami & Wardle 2005). Space-for-time substitution can take on a variety of forms. Typically, with broad-scale climate change research, an observed spatial relationship between an ecological response and a climatic predictor is used to model how an observed temporal gradient in the climatic predictor

would be likely to impact the ecological response (e.g. Currie 2001; Lemoine & Böhning-Gaese 2003; Lemoine *et al*. 2007*b*; Schaefer *et al*. 2008). Our first goal in this study is to assess the quality of space-for-time substitution as a predictive tool in broad-scale climate change research.

There is evidence that species within communities do not respond uniformly to the effects of modern climate change. For example, a relatively small subset of species have responded more rapidly to changing climatic conditions within communities of butterflies in Britain (Warren *et al*. 2001; Menéndez *et al*. 2006) and plants on Marion Island (le Roux & McGeoch 2008). Our second goal is to provide a broad-scale assessment of temporal trends in community structure and composition in order to determine whether changes have occurred, whether they are correlated with climatic trends and whether they represent evidence for a non-uniform response using the space-for-time predictions as a reference.

Here we examine trends in three community attributes from 1975 to 2001 for assemblages of terrestrial winter avifauna in North America. The attributes include species richness and two attributes summarized at the assemblage level: average body mass and average geographical occupancy. There is evidence that winter avifauna in North America has responded to climate change by shifting their distributions poleward (La Sorte & Thompson 2007). However, how these changes have been manifested within community composition and structure has yet to be determined. We formulate predictions using space-for-time substitution and assess how the three community attributes have changed over time relative to predictions

*Author for correspondence (flasorte@ucsd.edu).

1

and the level of evidence for causal associations with climate change using linear mixed models within a longitudinal study design.

2. MATERIAL AND METHODS

(a) *Data*

We used data from the North American Christmas Bird Count (CBC; National Audubon Society 2007) from 1975 to 2001 in our analysis. We chose 1975 as the starting date because observer effort became relatively consistent at that time. CBC surveys are conducted within 12 km radius circles for a period of 24 h during a two-week period centred on 25 December, representing a census of early winter avian assemblages. We included CBC circles that were sampled every year for which centres were more than 12 km from marine environments. Marine features were represented using a 1 km resolution global digital elevation model (GTOPO30; USGS 1996). We included CBC circles that had, from 1970 to 2000, less than 10 per cent gain in urban land cover within the 12 km radius circle. Land cover at CBC circles was estimated using the History Database of the Global Environment (HYDE v. 3.0) gridded at a 5 min resolution (approx. 9 km) and available at a 10-year interval (Goldewijk 2001, 2005). CBC circles are typically centred on towns or cities; therefore, urbanization represented the primary land-cover transformation with the strongest ecological impact likely to occur within CBC circles (McKinney 2002). A total of 404 CBC circles were considered, sampling regions in the contiguous USA and southern Canada, with a concentration of circles in the northeastern USA (electronic supplementary material, fig. S1). The 404 CBC circles contained a median of 3 per cent urban land cover in 1975 (range, 0.3–92.5%).

We included species in our analysis by first considering the 254 species examined by La Sorte & Thompson (2007). This investigation excluded species that were accidental or had winter ranges outside of the study area, were exclusively nocturnal or were associated with marine environments. We further refined this list by excluding species that were associated with freshwater environments or species that were partially nocturnal. We excluded freshwater species because they tend to be larger than terrestrial species, which could unduly skew our body-size distributions (Gaston & Blackburn 1995). We also excluded six species that showed evidence for extreme colonization or extirpation events based on changes in their distributions among CBC circles over time (La Sorte & Thompson 2007). These extreme events probably resulted from the direct and indirect consequences of a host of regional anthropogenic factors including land-use change, with climate change probably playing a secondary role. We excluded these species because the magnitude of these events would probably bias our results, making it difficult to detect a signal associated with climate change, which we predict to be relatively weak. This left 227 species for analysis (electronic supplementary material, table S1). Body mass for each species was acquired from Dunning (1984) and represents values averaged across male and female North American specimens.

Annual temperatures at CBC circles were estimated using a 30 min resolution (approx. 50 km) coverage of average monthly near-surface temperature for the period 1975–2001 (CRU TS 2.1; Mitchell & Jones 2005). The monthly values were averaged for each year and extracted for each 12 km radius CBC circle based on the grid cell where the circle was centred. We chose annual temperature over winter temperature because the level of annual variability was considerably lower for annual temperature (electronic supplementary material, fig. S2). The reduction in annual variability resulted in statistical associations that were less sensitive to adjustments in the data and models.

(b) *Analysis*

We examined the impact of climate change on three attributes of community structure and composition: species richness, body mass and occupancy. Species richness was the total number of species documented at a CBC circle during a survey. Body mass was log transformed and averaged across species documented during a survey. Occupancy was based on the number of CBC circles at which a species occurred annually. These values were averaged across species documented during a survey. To account for a potential spatial bias in our measure of occupancy based on the distributions of CBC circle locations (electronic supplementary material, fig. S1), we repeated all analyses on a random subset of circles that were distributed uniformly across North America. Survey effort (the number of party hours per survey) was found to have a linear association on a log scale with each of the three community attributes: a positive association with species richness and a negative association with body mass and occupancy. We therefore included log-transformed survey effort as a covariate in our models to account for the effect of temporal and spatial differences in survey effort within and among CBC circles.

We used indirect space-for-time substitution (Fukami & Wardle 2005) to predict how the three community attributes would be likely to change over time in association with observed changes in annual temperature. Indirect space-for-time substitution uses the observed spatial relationship between an ecological response (community attribute) and a predictor (annual temperature) to model how an observed temporal gradient in the predictor would be likely to impact the response. All factors were averaged over the first 3 years of the survey (1975–1977) and ordinary least-squares (OLS) regression was used to examine the structure of the spatial relationships. This 3-year period was used because OLS regression coefficients derived from averaging sequentially greater numbers of years stabilized and entered a monotonic relationship after approximately 3 years (electronic supplementary material, fig. S3). Survey effort on a log scale was averaged over the same time period and included as a covariate in the models. To derive the temporal predictions for the space-for-time substitution, the coefficients from the OLS models were used to predict annual values for each of the three community attributes based on annual temperatures observed at each CBC circle from 1975 to 2001. We examined the relationship between the accuracy of the temporal predictions for each community attribute and the statistical quality of the OLS models. We also estimated the contribution of unexplained spatial-structured variation within the residuals for each model using simultaneous autoregressive models and pseudo-R^2 values (Kissling & Carl 2008). Thus, statistical deviations from OLS model assumptions were considered a legitimate part of our assessment.

We used linear mixed models to assess how the three community attributes had changed over time, and linear mixed models within a longitudinal study design (Fitzmaurice *et al.* 2004) to assess the correlation between trends in the

three community attributes and observed trends in annual temperature. The linear mixed models included predictors that represent changes occurring within CBC circles over time (time-varying or longitudinal effects) and predictors that represent baseline differences between CBC circles across space (time-stationary or cross-sectional effects). We achieved simultaneous inference for the longitudinal and cross-sectional effects by subtracting baseline values for each predictor from its longitudinal values (Fitzmaurice *et al.* 2004, pp. 418–422). To account for CBC circle-specific effects, we included CBC circle as a random effect with randomly varying intercepts and slopes for year. Fixed effects included year (with 1975 set as zero), annual values at each CBC circle for temperature and survey effort (longitudinal effects), and 1975 values for temperature and survey effort (cross-sectional effect). The distributional assumptions for the within-circle errors and random effects estimated for each circle were found to be valid for all three community attributes.

The longitudinal study design allowed us to assess the association between changes in the three community attributes with changes in temperature after controlling for baseline or spatial differences between CBC circles. The implied causal interpretations for the longitudinal effects are dependent on the assumption that the predictors are external with respect to the response (Fitzmaurice *et al.* 2004, pp. 418–422). That is, the predictors are time-varying, stochastic and conditional on their own past values, but future values cannot be predicted by past values of species richness, body mass or occupancy. It is likely that this assumption is valid for annual temperature, which is external to our study system. Therefore, we treat significant longitudinal effects for temperature as providing evidence for causal associations.

We used partial residual plots to display the spatial and temporal associations for the three community attributes (Larsen & McCleary 1972). This technique allowed us to present associations after accounting for survey effort and CBC circle-specific effects. The partial residuals are defined by

$$r_i^* = r_i + bx_i$$

where r_i is the ordinary residual for the *i*th observation, b is the coefficient for annual temperature in the spatial OLS regression models and for year in the linear mixed models, and x_i is the *i*th observation for annual temperature in the spatial OLS regression models and the *i*th value for year in the linear mixed models. The partial residual plots are plots of r_i^* versus x_i and are presented independently for each of the three community attributes. We implemented our analysis in R v. 2.8.1 (R Development Core Team 2009) using the function lme available in the nlme library to implement the linear mixed models (Pinheiro & Bates 2000) and the spdep library to implement the simultaneous autoregressive models.

3. RESULTS

After accounting for differences in survey effort among the CBC circles, the associations between the three community attributes and annual temperature during 1975–1977 revealed distinct spatial relationships (figure 1; table 1). Species richness had a significant positive association with temperature; conversely, body mass and occupancy had significant negative associations with temperature. Thus, across the CBC circles, higher
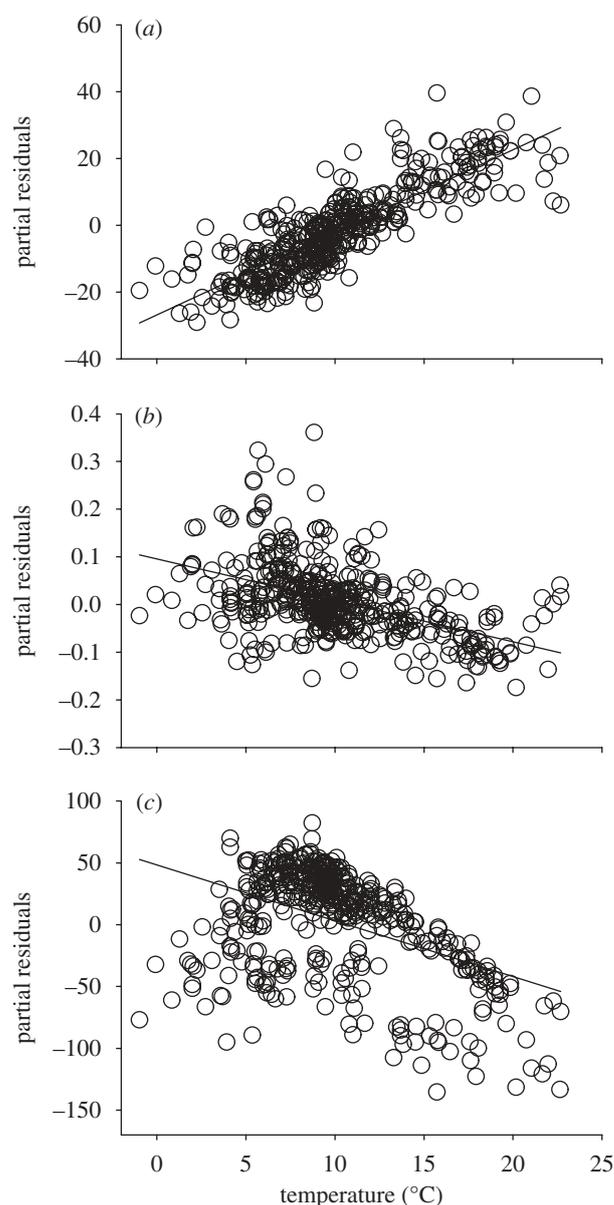
Figure 1. Observed spatial associations. Partial residuals from the OLS regression of three community attributes ((*a*) species richness, $R^2 = 0.79$; (*b*) body mass, $R^2 = 0.25$; (*c*) occupancy, $R^2 = 0.20$) by annual temperature for 404 North American CBC circles containing a total of 227 species. The partial residuals represent spatial trends after controlling for differences in survey effort among CBC circles. All variables used in the analysis were averaged over 1975–1977 for each CBC circle. Body mass is on a log scale.

annual temperatures were associated with greater numbers of species, and species that were smaller on average with lower occupancy on average. Based on model quality and the amount of spatial variation in each attribute explained by annual temperature (figure 1), temperature was a much better predictor of species richness, followed by body mass and occupancy. Residual variation explained by each attribute's spatial structure was approximately 4 per cent for species richness, 14 per cent for body mass and 62 per cent for occupancy.

Annual temperature at the CBC circles increased $0.03°C \, yr^{-1}$ on average ($t_{10503} = 39.14$; $p \leq 0.001$), representing an overall gain of $0.93°C$ on average from 1975 to 2001 (figure 2). After accounting for survey

Table 1. Observed spatial associations. Regression coefficients and test statistics for OLS regression examining spatial relationships between three community attributes and annual temperature (T) after controlling for survey effort (E) for 404 CBC circles containing a total of 227 species. All factors were averaged over the period 1975–1977. Coefficients with $p \leq 0.05$ are shown in bold.

	coefficient	s.e.	t	p-value
species richness				
intercept	**−17.7726**	2.1655	−8.21	0.0000
T	**2.4521**	0.0817	30.03	0.0000
E	**9.8339**	0.5330	18.45	0.0000
body mass				
intercept	**1.8880**	0.0217	87.09	0.0000
T	**−0.0081**	0.0008	−9.96	0.0000
E	**−0.0211**	0.0053	−3.95	0.0001
occupancy				
intercept	**337.7704**	12.7606	26.47	0.0000
T	**−4.5690**	0.4813	−9.49	0.0000
E	−6.1309	3.1408	−1.95	0.0516

Table 2. Observed temporal associations. Regression coefficients and test statistics for linear mixed models examining changes in three community attributes after controlling for survey effort for 404 North American CBC circles from 1975 to 2001 containing a total of 227 species. The mixed models are based on a longitudinal study design with year representing the temporal component. The models include longitudinal (E) and cross-sectional effects (E_{1975}). Coefficients with $p \leq 0.05$ are shown in bold.

	coefficient	s.e.	t	p-value
species richness				
intercept	−1.0942	3.4166	−0.32	0.7488
year	**0.0527**	0.0107	4.93	0.0000
E	**5.4429**	0.1302	41.82	0.0000
E_{1975}	**11.8373**	0.8411	14.07	0.0000
body mass				
intercept	**1.8422**	0.0192	95.77	0.0000
year	**0.0004**	0.0001	4.79	0.0000
E	**−0.0030**	0.0014	−2.07	0.0383
E_{1975}	**−0.0299**	0.0047	−6.33	0.0000
occupancy				
intercept	**323.3544**	12.6362	25.59	0.0000
year	**0.3650**	0.0246	14.86	0.0000
E	**−9.2868**	0.3716	−24.99	0.0000
E_{1975}	**−14.4404**	3.1097	−4.64	0.0000

Figure 2. Annual temperature observed at 404 North American CBC circles averaged annually ($\pm$ s.e.). The values are connected sequentially (dashed line), and the trend was estimated using a linear mixed model that controlled for CBC circle-specific effects (solid line).

effects, predicted trends for all three community attributes differed significantly from observed trends (figure 3). The predicted trend for species richness was positive and stronger than the observed trend, and the predicted trends for body mass and occupancy were both negative in contrast to observed positive trends. The quality of the spatial relationship for each community attribute (figure 1) directly mirrored its predictive strength (figure 3), with species richness having the strongest predictive power followed sequentially by body mass and occupancy.

Evidence for causal associations between two of the three community attributes and annual temperature were suggested based on the longitudinal analysis (table 3). After accounting for survey effort and CBC circle-specific effects, the longitudinal effect of temperature had positive associations with species richness and body mass; occupancy lacked significant associations. Hence, there was evidence for a causal relationship between the positive trends in temperature and positive trends in species richness and body mass. We tested for a potential spatial bias in our longitudinal analysis by randomly selecting 123 CBC circles from the 404 that occurred uniformly across the study area (see table S2 in the electronic supplementary material for details). We found identical associations across all three attributes including occupancy, suggesting the lack of a spatial bias in our analysis.

4. DISCUSSION

After accounting for possible effects of land-use change and survey effort, our findings indicate a general trend of increasing species richness, average body mass and average geographical occupancy for assemblages of terrestrial winter avifauna in North America from 1975 to 2001. Species richness presented the broadest support for a causal association with climate change based on a general concurrence with space-for-time predicted trends and a correlation with observed trends in annual temperature. Body mass and especially occupancy showed poorer support: trends in body mass were correlated with observed

effort and CBC circle-specific effects, positive temporal trends in the three community attributes were evident (figure 3; table 2). Species richness increased annually by 0.05 species on average; median body mass had an annual multiplicative increase of 1.001 g or an annual gain of 0.09 per cent; and occupancy increased by 0.37 circles annually. Hence, all three community attributes presented positive temporal trends that were statistically significant.

When the spatial relationships were applied to the observed trends in temperature, the space-for-time substitution generated predictions on how the community attributes would be expected to change over time (figure 3). After accounting for survey effort and CBC circle-specific
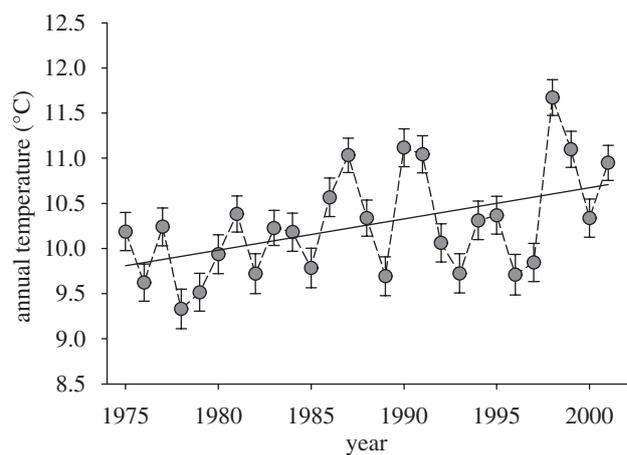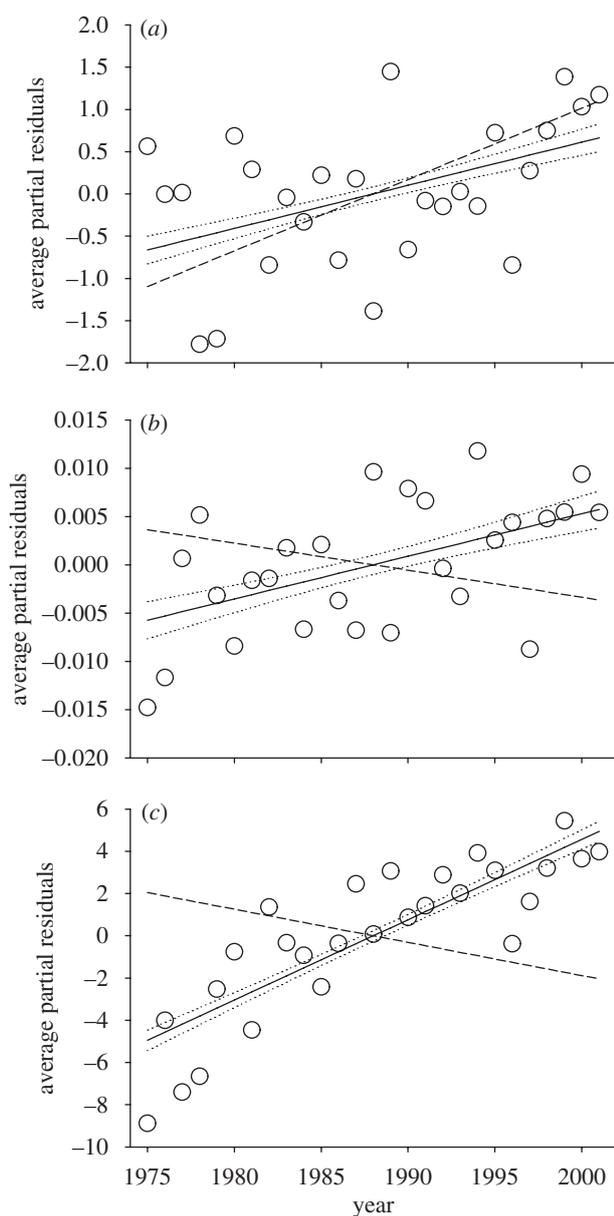
Figure 3. Observed and predicted temporal associations. Partial residuals averaged annually from linear mixed models examining observed (solid line) and predicted (dashed line) trends in three community attributes ((*a*) species richness, (*b*) body mass, (*c*) occupancy) from 1975 to 2001 for 404 North American CBC circles containing a total of 227 species. The partial residuals represent temporal trends after controlling for differences in survey effort and CBC circle-specific effects. Observed trends include 95 per cent confidence bands (dotted lines). The predicted trends were estimated using space-for-time substitution. Body mass is on a log scale.

trends in annual temperature but not with predicted trends, and occupancy showed no correlation with observed trends in annual temperature or with predicted trends. Our results suggest that modern global climate change is associated with community-level changes that cannot be comprehensively predicted using spatial ecological associations. This outcome suggests that space-for-time substitution has limited applicability as a predictive tool under climate change and also suggests that species within communities are responding in a non-uniform manner to climate change.

Table 3. Climate change causal associations. Regression coefficients and test statistics for linear mixed models examining changes in three community attributes and their association with changes in annual temperature after controlling for survey effort for 404 North American CBC circles from 1975 to 2001 containing a total of 227 species. The mixed models are based on a longitudinal study design with year representing the temporal component. The models include longitudinal effects for temperature (T) and survey effort (E) and cross-sectional effects for temperature (T_{1975}) and survey effort (E_{1975}). Coefficients with $p \leq 0.05$ are shown in bold.

	coefficient	s.e.	t	p-value
species richness				
intercept	**−12.1898**	2.0709	−5.89	0.0000
year	**0.0409**	0.0108	3.78	0.0002
T	**0.3459**	0.0486	7.12	0.0000
T_{1975}	**2.2712**	0.0805	28.23	0.0000
E	**5.4652**	0.1295	42.20	0.0000
E_{1975}	**8.6742**	0.5137	16.89	0.0000
body mass				
intercept	**1.8870**	0.0159	118.83	0.0000
year	**0.0003**	0.0001	3.82	0.0001
T	**0.0023**	0.0006	4.05	0.0001
T_{1975}	**−0.0093**	0.0006	−15.22	0.0000
E	**−0.0031**	0.0014	−2.17	0.0301
E_{1975}	**−0.0165**	0.0039	−4.22	0.0000
occupancy				
intercept	**340.1503**	12.0222	28.29	0.0000
year	**0.3682**	0.0250	14.71	0.0000
T	−0.0972	0.1419	−0.68	0.4934
T_{1975}	**−3.9039**	0.4675	−8.35	0.0000
E	**−9.2766**	0.3720	−24.93	0.0000
E_{1975}	**−8.3926**	2.9822	−2.81	0.0051

Space-for-time substitution is becoming an increasingly common tool in ecological climate change research. For example, the correspondence between predicted and observed ecological trends has been used to bolster claims of a causal association with climate change (Lemoine & Böhning-Gaese 2003; Lemoine *et al.* 2007*b*), and ecological trends have been extrapolated into the future based on climate change projections (Currie 2001; Schaefer *et al.* 2008). Our findings provide evidence that, when examined at the community level over a large geographical extent, temporal trends in community attributes do not always conform to trends predicted on the basis of observed spatial gradients, and this outcome occurs even when trends in the community attributes are correlated with observed climatic trends. In addition, we found evidence that the quality of the spatial model was directly related to the accuracy of the temporal predictions. The implication is that, when applying space-for-time substitution, investigators should carefully consider the nature and quality of the spatial relationship under consideration. This includes both the statistical quality of the relationship and the level of spatial autocorrelation displayed by the ecological response.

Space-for-time substitution is a valuable ecological tool. However, using spatial relationships that were established over millennia to model the ecological consequences of modern climatic change, which is occurring at a relatively rapid rate, appears to be problematic. In general, our findings put into question the application

of space-for-time substitution when searching for evidence of causal associations. This approach might be justified in some cases, as we found with species richness where observed trends were correlated with trends in temperature, and this association was corroborated at a general level by predicted trends. However, as we found with body mass, strong differences in observed and predicted trends, which would suggest no causal association, were not supported by the observed temporal associations with temperature. Our findings also put into question the extrapolation of spatial trends into the future. Predicted trends diverged significantly from observed trends for all three community attributes, indicating that the level of uncertainty associated with long-term extrapolation could be substantial.

Based on well-studied latitudinal patterns, we would expect species richness, body mass and occupancy to have certain spatial associations with temperature. These spatial associations were supported by our spatial analysis, including Bergmann's rule (see the review by Gaston *et al.* 2008), where we would expect increasing temperature to be associated with lower average body mass. Bergmann's rule is supported geographically at the intraspecific level for the majority of bird species (Ashton 2002) and for assemblages of the New World birds (Blackburn & Gaston 1996; Ramirez *et al.* 2008). The strongest agreement geographically with the rule has been found for winter distributions of the New World birds (Ramirez *et al.* 2008), where temperature has been found to be an important factor defining avian distributional limits (Root 1988).

There is evidence that body mass of individual species has changed in response to climate change; however, these trends are not always in agreement with Bergmann's rule, suggesting that the predictive power of Bergmann's rule for trends at the intraspecific level is limited (Millien *et al.* 2006). It has been suggested that the predictive power for trends at the assemblage level, particularly at broader spatial scales, might be more consistent (Millien *et al.* 2006). The assemblage form, however, is rarely applied to well-delineated assemblages; in the majority of cases, assemblages are defined in an arbitrary fashion, typically based on overlapping gridded range maps (Meiri & Thomas 2007; Gaston *et al.* 2008). Therefore, our findings provide evidence that trends in assemblage-level body mass under climate change for well-defined assemblages do not conform to the expectations of Bergmann's rule.

Based on species richness latitudinal gradients (reviewed by Willig *et al.* 2003), we would expect temperature and species richness to be positively correlated across space. We would also expect there to be a similar temporal effect, where increasing temperatures would be associated with increasing species richness, an outcome that has been found for butterflies and marine fishes (Menéndez *et al.* 2006; Hiddink & ter Hofstede 2008). The observed spatial and temporal trends in species richness follow both these expectations. In addition, geographical variation in species richness is typically negatively correlated with average body mass (Meiri & Thomas 2007), a relationship that has been documented with New World birds (Blackburn & Gaston 1996). These spatial associations suggest that gains in species richness over time should be reciprocated by losses in

average body mass. We found no evidence to support this prediction. Finally, based on Rapoport's rule (Stevens 1989)—which finds its best support at high latitudes in the Northern Hemisphere (Gaston *et al.* 1998)—we would expect increasing temperatures across space and time to be associated with decreasing range size for assemblages of winter avifauna in North America. The observed spatial trend followed this expectation, but the observed temporal trend diverged substantially from this expectation.

An explanation for the divergence between observed and predicted trends for body mass and occupancy requires the consideration of several factors. The first is the evidence that increasing winter temperatures have resulted in larger-bodied individuals, a phenomenon thought to be a consequence of species diverting energy from maintenance to growth (Millien *et al.* 2006). At the community level, this explanation would be characterized by the increased prevalence of larger-bodied species that are able to take advantage of the unique resource opportunities associated with climate change. When examining species whose geographical distributions have shifted under climate change, habitat availability and dispersal capacity have been found to be important factors (Pöyry *et al.* 2009). There is evidence for range shifts for winter avifauna in North America (La Sorte & Thompson 2007); considering that larger-bodied species tend to have broader ecological niches and broader geographical distributions than smaller-bodied species (Gaston & Blackburn 2000), and larger-bodied species tend to be better active dispersers (Jenkins *et al.* 2007), it could be argued that larger-bodied species are in a better position, at least initially through dispersal, to respond to changing climatic conditions (Warren *et al.* 2001; Menéndez *et al.* 2006).

A second factor would involve changes in biotic interactions as community composition responds to shifts in species' geographical distributions. Biotic interactions under a variety of observational, experimental and theoretical settings have been found to play a significant role determining how species' distributions are structured and how they will be likely to respond to climate change (Davis *et al.* 1998; Anderson *et al.* 2002; Heegaard & Vandvik 2004; Araújo & Luoto 2007; Brooker *et al.* 2007; Heikkinen *et al.* 2007). A third factor would include spatial variation in the response of species and communities to changing climates (Visser *et al.* 2003; Genner *et al.* 2004), which could result in outcomes that, when summarized geographically, could differ from historic associations. A final factor would involve land-use change that, even at the levels included in this study, could provide the conditions necessary for large-bodied species to increase in prevalence. Overall, the observed trends could represent a 'temporary' phenomenon resulting from the opportunistic response of specific species that, ecologically, are in a better position to take advantage of changing local and regional biotic and abiotic conditions. If the effects of land-use change are not significant, and if given enough time, it is conceivable that historic associations could be re-established (Menéndez *et al.* 2006). Alternatively, the trends could represent a novel consequence of anthropogenic global change with unprecedented long-term implications (Williams & Jackson 2007).

In summary, our findings indicate that ecological trends were evident at the community level for winter

avifauna, and aspects of these trends were associated with climate change. However, the observed trends and causal associations were not completely confirmed by predicted trends, suggesting that space-for-time substitution is not a comprehensive predictive tool at the community level. Nevertheless, because of the lack of high-quality temporal databases for many geographical regions and taxonomic groups, space-for-time substitution is likely to see greater and more widespread applications. This is particularly true as interest in documenting and modelling the ecological impact of climate change increases. However, our findings indicate that care must be taken in the use of this method and suggest that climate change might result in unexpected ecological consequences as species and communities respond to changing climates. As our results suggest, the broad-scale ecological impact of climate change on biological communities can be detected even over relatively short time periods ($<$30 years). If we intend to accurately document the impacts of global change and predict the long-term consequences for biodiversity and ecosystem services, our study reinforces the importance of maintaining long-term and broad-scale ecological monitoring programmes.

REFERENCES

Anderson, R. P., Peterson, A. T. & Gómez-Laverde, M. 2002 Using niche-based GIS modeling to test geographic predictions of competitive exclusion and the competitive release in South American pocket mice. *Oikos* **98**, 3–16. (doi:10.1034/j.1600-0706.2002.t01-1-980116.x)

Araújo, M. B. & Luoto, M. 2007 The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* **16**, 743–753. (doi:10.1111/j.1466-8238.2007.00359.x)

Ashton, K. G. 2002 Patterns of within-species body size variation of birds: strong evidence for Bergmann's rule. *Glob. Ecol. Biogeogr.* **11**, 505–523. (doi:10.1046/j.1466-822X.2002.00313.x)

Blackburn, T. M. & Gaston, K. J. 1996 Spatial patterns in the body sizes of bird species in the New World. *Oikos* **77**, 436–446. (doi:10.2307/3545933)

Brooker, R. W., Travis, J. M. J., Clark, E. J. & Dytham, C. 2007 Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *J. Theor. Biol.* **245**, 59–65. (doi:10.1016/j.jtbi.2006.09.033)

Currie, D. J. 2001 Projected effects of climate change on patterns of vertebrate and tree species richness in the conterminous United States. *Ecosystems* **4**, 216–225. (doi:10.1007/s10021-001-0005-4)

Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B. & Wood, S. 1998 Making mistakes when predicting shifts in species ranges in response to global warming. *Nature* **391**, 783–786. (doi:10.1038/35842)

Dunne, J. A., Saleska, S. R., Fischer, M. L. & Harte, J. 2004 Integrating experimental and gradient methods in ecological climate change research. *Ecology* **85**, 904–616. (doi:10.1890/03-8003)

Dunning, J. B. J. 1984 *Body weights of 686 species of North American birds*. Cave Creek, AZ: Western Bird Banding Association. Monograph no. 1. Eldon Publishing.

Fitzmaurice, G. M., Laird, N. M. & Ware, J. H. 2004 *Applied longitudinal analysis*. Hoboken, NJ: Wiley & Sons.

Fukami, T. & Wardle, D. A. 2005 Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proc. R. Soc. B* **272**, 2105–2115. (doi:10.1098/rspb.2005.3277)

Gaston, K. J. & Blackburn, T. M. 1995 The frequency-distribution of bird body weights—aquatic and terrestrial species. *Ibis* **137**, 237–240. (doi:10.1111/j.1474-919X.1995.tb03245.x)

Gaston, K. J. & Blackburn, T. M. 2000 *Pattern and process in macroecology*. Oxford, UK: Blackwell Science.

Gaston, K. J., Blackburn, T. M. & Spicer, J. I. 1998 Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* **13**, 70–74. (doi:10.1016/S0169-5347(97)01236-6)

Gaston, K. J., Chown, S. L. & Evans, K. L. 2008 Ecogeographical rules: elements of a synthesis. *J. Biogeogr.* **35**, 483–500. (doi:10.1111/j.1365-2699.2007.01772.x)

Genner, M. J., Sims, D. W., Wearmouth, V. J., Southall, E. J., Southward, A. J., Henderson, P. A. & Hawkins, S. J. 2004 Regional climatic warming drives long-term community changes of British marine fishes. *Proc. R. Soc. Lond. B* **271**, 655–661. (doi:10.1098/rspb.2003.2651)

Goldewijk, K. K. 2001 Estimating global land use change over the past 300 years: the HYDE database. *Glob. Biogeochem. Cycles* **15**, 417–433. (doi:10.1029/1999GB001232)

Goldewijk, K. K. 2005 Three centuries of global population growth: a spatial referenced population (density) database for 1700–2000. *Popul. Environ.* **26**, 343–367. (doi:10.1007/s11111-005-3346-7)

Heegaard, E. & Vandvik, V. 2004 Climate change affects the outcome of competitive interactions—an application of principle response curves. *Oecologia* **139**, 459–466. (doi:10.1007/s00442-004-1523-5)

Heikkinen, R. K., Luoto, M., Virkkala, R., Pearson, R. G. & Körber, J. 2007 Biotic interactions improve prediction of boreal bird distributions at macro-scales. *Glob. Ecol. Biogeogr.* **16**, 754–763. (doi:10.1111/j.1466-8238.2007.00345.x)

Hiddink, J. G. & ter Hofstede, R. 2008 Climate induced increases in species richness of marine fishes. *Glob. Change Biol.* **14**, 453–460. (doi:10.1111/j.1365-2486.2007.01518.x)

Jenkins, D. G. *et al.* 2007 Does size matter for dispersal distance? *Glob. Ecol. Biogeogr.* **16**, 415–425. (doi:10.1111/j.1466-8238.2007.00312.x)

Jetz, W., Wilcove, D. S. & Dobson, A. P. 2007 Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biol.* **5**, 1211–1219. (doi:10.1371/journal.pbio.0050157)

Karl, T. R. & Trenberth, K. E. 2003 Modern global climate change. *Science* **302**, 1719–1723. (doi:10.1126/science.1090228)

Kissling, W. D. & Carl, G. 2008 Spatial autocorrelation and the selection of simultaneous autoregressive models. *Glob. Ecol. Biogeogr.* **17**, 59–71.

Lambin, E. F. & Geist, H. 2006 *Land-use and land-cover change*. Berlin, Germany: Springer.

Larsen, W. A. & McCleary, S. J. 1972 The use of partial residual plots in regression analysis. *Technometrics* **14**, 781–790. (doi:10.2307/1267305)

La Sorte, F. A. & Thompson, F. R. 2007 Poleward shifts in winter ranges of North American birds. *Ecology* **88**, 1803–1812. (doi:10.1890/06-1072.1)

Lemoine, N. & Böhning-Gaese, K. 2003 Potential impact of global climate change on species richness of long-distance migrants. *Conserv. Biol.* **17**, 577–586. (doi:10.1046/j.1523-1739.2003.01389.x)

Lemoine, N., Bauer, H. G., Peintinger, M. & Böhning-Gaese, K. 2007*a* Effects of climate and land-use change on species abundance in a central European bird community. *Conserv. Biol.* **21**, 495–503. (doi:10.1111/j.1523-1739.2006.00633.x)

Lemoine, N., Schaefer, H. C. & Böhning-Gaese, K. 2007*b* Species richness of migratory birds is influenced by global climate change. *Glob. Ecol. Biogeogr.* **16**, 55. (doi:10.1111/j.1466-8238.2006.00252.x)

le Roux, P. C. & McGeoch, M. A. 2008 Rapid range expansion and community reorganization in response to warming. *Glob. Change Biol.* **14**, 2950–2962. (doi:10.1111/j.1365-2486.2008.01687.x)

McKinney, M. L. 2002 Urbanization, biodiversity, and conservation. *Bioscience* **52**, 883–890. (doi:10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2)

Meiri, S. & Thomas, G. H. 2007 The geography of body size—challenges of the interspecific approach. *Glob. Ecol. Biogeogr.* **16**, 689–693. (doi:10.1111/j.1466-8238.2007.00343.x)

Menéndez, R., Megías, A. G., Hill, J. K., Braschler, B., Willis, S. G., Collingham, Y., Fox, R., Roy, D. B. & Thomas, C. D. 2006 Species richness changes lag behind climate change. *Proc. R. Soc. B* **273**, 1465–1470. (doi:10.1098/rspb.2006.3484)

Millien, V., Lyons, S. K., Olson, L., Smith, F. A., Wilson, A. B. & Yom-Tov, Y. 2006 Ecotypic variation in the context of global climate change: revisiting the rules. *Ecol. Lett.* **9**, 853–869. (doi:10.1111/j.1461-0248.2006.00928.x)

Mitchell, T. D. & Jones, P. D. 2005 An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.* **25**, 693–712. (doi:10.1002/joc.1181)

National Audubon Society 2007 The Christmas Bird Count Historical Results. See http://www.audubon.org/bird/cbc; date accessed: 10 February 2008.

Pickett, S. T. A. 1987 Space-for-time substitution as an alternative. In *Long-term studies in ecology: approaches and alternatives* (ed. G. E. Likens), pp. 110–135. New York, NY: Springer-Verlag.

Pinheiro, J. C. & Bates, D. M. 2000 *Mixed-effects models in S and S-PLUS*. New York, NY: Springer.

Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M. & Saarinen, K. 2009 Species traits explain recent range shifts of Finnish butterflies. *Glob. Change Biol.* **15**, 732–743. (doi:10.1111/j.1365-2486.2008.01789.x)

R Development Core Team 2009 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See http://www.R-project.org.

Ramirez, L., Diniz, J. A. F. & Hawkins, B. A. 2008 Partitioning phylogenetic and adaptive components of the geographical body-size pattern of New World birds. *Glob. Ecol. Biogeogr.* **17**, 100–110.

Root, T. L. 1988 Environmental factors associated with avian distributional boundaries. *J. Biogeogr.* **15**, 489–505. (doi:10.2307/2845278)

Sala, O. E. *et al.* 2000 Global biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774. (doi:10.1126/science.287.5459.1770)

Schaefer, H.-C., Jetz, W. & Böhning-Gaese, K. 2008 Impact of climate change on migratory birds: community reassembly versus adaption. *Glob. Ecol. Biogeogr.* **17**, 38–49.

Stevens, G. C. 1989 The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256. (doi:10.1086/284913)

USGS 1996 *GTOPO30—global topographic data*. Sioux Falls, SD: United States Geological Survey, EROS Data Center Distributed Active Archive Center (EDC DAAC).

Visser, M. E. *et al.* 2003 Variable responses to large-scale climate change in European *Parus* populations. *Proc. R. Soc. Lond. B* **270**, 367–372. (doi:10.1098/rspb.2002.2244)

Warren, M. S. *et al.* 2001 Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* **414**, 65–69. (doi:10.1038/35102054)

Williams, J. W. & Jackson, S. T. 2007 Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5**, 475–482. (doi:10.1890/070037)

Willig, M. R., Kayfman, D. M. & Stevens, R. D. 2003 Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annu. Rev. Ecol. Evol. Syst.* **34**, 273–309. (doi:10.1146/annurev.ecolsys.34.012103.144032)