Climate tolerance and interspecific variation in geographic range size

Jason Pither

Department of Biology, Queen's University, Kingston, Ontario K7L 3N6, Canada (pitherj@biology.queensu.ca)

The fact that climate influences the continental-scale distributions of species is one of the central tenets of ecology and biogeography. Equally elemental is that species exhibit enormous variation in geographic range size, with most occupying comparatively small areas. The degree to which climate can account for this variation remains unclear. Here, I test three alternative climate-based hypotheses for variation in range size using a large sample of tree and shrub species native to North America north of Mexico. I show that the lowest value of January average daily minimum temperature encompassed by a species' geographic range (T_{MIN}), representing the 'climate extremes hypothesis', explains almost 80% of the variation in range size. Hypotheses based on seasonality and climate optima find substantially less support. The relationship between range size and T_{MIN} does not change across the breadth of latitudes examined, and is general for conifers and hardwoods, and growth form (tree versus shrub). Differential freezing resistance gains support as the mechanism underlying interspecific variation in range size: using 35 species for which data were available, both T_{MIN} and range size are shown to be strongly correlated with measures of freezing resistance.

Keywords: geographic range size; physiological tolerance; macroecology; tree biogeography; climate variability hypothesis

1. INTRODUCTION

Understanding what governs the distributions of species is a central goal of ecology and biogeography (Rosenzweig 1995). A significant contribution to this goal would be to determine what factors underlie the remarkable variation in range size exhibited by most taxonomic groups (Gaston 1994). Many potential mechanisms have been proposed (reviewed in Brown *et al.* 1996; Gaston 1996, 1998), but they have yet to be ascribed relative importance (Brown 1999; Gaston 1999; Rohde 1999; but see Bell 2001; Gaston & He 2002). Climate tolerance is thought to play a dominant role in extra-tropical regions, especially for plant (Woodward 1987; Latham & Ricklefs 1993; Dynesius & Jansson 2000) and insect taxa (see, for example, Farrell & Mitter 1993). Indeed, 'climate response surfaces' are routinely and successfully used to provide probabilistic maps of plant (see, for example, Shafer *et al.* 2001) and insect (see, for example, Hill *et al.* 1999) species' distributions for given regions. What remains unclear is the degree to which climatic parameters account for the large amount of interspecific variation in range size that is typical of most taxonomic assemblages, and further, what mechanisms underlie any such relationships. Recent research (e.g. Letcher & Harvey 1994; Hughes *et al.* 1996; Cowlshaw & Hacker 1997; Gaston & Chown 1999a; Addo-Bediako *et al.* 2000) has focused on Stevens' 'climate variability hypothesis' (CVH) (Stevens 1989), which suggests that species able to tolerate large magnitudes of climatic variability (e.g. large annual temperature ranges, figure 1a) at any locality possess climate-generalist habits that should permit occupancy of larger geographical areas than species with narrow climate tolerances. The CVH was originally formulated as a potential explanation for Rapoport's rule: the trend of increasing range size with increasing latitude (Stevens 1989), which itself formed a component of an

explanation for latitudinal gradients in species richness (Stevens 1989). Since Stevens' influential paper, latitudinal gradients in range size have been shown to be the exception rather than the rule (reviewed in Gaston *et al.* 1998; Rohde 1999), although more studies that properly address the methodological and spatial complexities of the system are certainly warranted (Rohde 1999). Here, I seek an explanation for general gradients in range size, of which latitudinal gradients simply form a special case.

Climate-based hypotheses for variation in range size include both evolutionary and ecological components: species have evolved differing climatic optima and ranges of climatic tolerance, while patterns of climate through time and space provide complex mosaics of climate suitability that influence population-level processes. Therefore (i) knowledge of both historical and contemporary patterns of climate and species' distributions (Webb & Bartlein 1992), (ii) data concerning the physiological tolerances of the species (Chown & Gaston 1999), and (iii) analytical methods that account for the spatial complexity of the data would each contribute substantially to assessments of climate tolerance as an explanation for variation in range size.

I evaluate climatic correlates of range size using a large sample of tree and shrub species native to North America north of Mexico. This assemblage is ideal because the species' ranges are mapped with relatively high accuracy (Little 1971, 1976, 1977) and are available in digital format, enabling spatially explicit analyses in a geographical information system (GIS) (see § 2; figure 1a inset), the frequency distribution of their range sizes is typical (figure 2), there exists a good spatial coverage of climate data for the entire study extent, there is considerable knowledge concerning the evolutionary (and more recent) history of tree species within the continent (Barkley *et al.* 1993; Qian & Ricklefs 1999), and the physiological ecology of

Figure 1. (a) Average annual temperature range, and (b) average January daily minimum temperatures ($^{\circ}\text{C}$). Contours were calculated in the ARCVIEW GIS using inverse distance weighted interpolation of data from 5521 climate stations. The inset figure in (a) illustrates how the multi-polygon geographic range (in light grey) of giant chinkapin (*Castanopsis chrysophylla*) encompasses 42 climate stations (bolder black points) within the GIS overlay procedure. The smaller points outside the grey shading are climate stations in the region that are not encompassed by the range. The lower black open circle is centred on the station that provided the single highest value of average annual temperature range (T_{MAXRANGE}) used in the analyses for this species, whereas the upper black open circle corresponds to the source for the lowest value of average January daily minimum temperature (T_{MIN}). In (b) more than 60% of the land area experiences average January minimum temperatures below -10°C , and more than 85% experiences temperatures below freezing. The maps are presented in a Lambert equal area azimuthal projection.

many species in the group (see, for example, Sakai & Weiser 1973), and woody plants in general (see, for example, Parker 1963; Woodward 1987), is well understood.

In addition to the CVH (described above), I test the following hypotheses for variation in range size (table 1): the 'climate extremes hypothesis' (CEH) states that climatic extremes (as indexed, for example, by the average

Figure 2. The range-size distribution (here represented as non-transformed proportional areas) for the 103 tree species used in the analyses. Proportional areas varied from 0.12% (*Chamaecyparis lawsoniana*) to 37.3% (*Betula papyrifera*) of the land area of North America north of Mexico. The roman numerals refer to each of the following features of the distribution and are discussed in the text: (i) the breadth and variance of range sizes; (ii) the maximum range size; (iii) the low frequencies of large ranges; and (iv) the mode occurring at small range sizes.

January daily minimum temperature; figure 1b) located within the range may relate to range size in a way analogous to that proposed by the CVH (Gaston & Chown 1999a,b; Addo-Bediako *et al.* 2000). In particular, freezing tolerance has been implicated as a factor influencing the limits of tree species' ranges (e.g. Sakai & Weiser 1973; Woodward 1987; Latham & Ricklefs 1993; Aizen & Woodcock 1996; Loehle 1998), and species that are tolerant of extreme cold at any single locality may be able to occupy a larger area than those that are intolerant. This is especially relevant for regions such as North America north of Mexico, where below-freezing winter temperatures dominate (figure 1b and caption). The 'optimal climate hypothesis' (OCH) states that species may experience some optimum level of climate conditions (including seasonality) such that the averages of climate measures calculated from throughout the species' range (rather than single extreme values) are best correlated with range size (cf. Hughes *et al.* 1996). Each of these hypotheses assumes that tree species' ranges are in relative equilibrium with contemporary climate (Huntley 1991; McGlone 1996; Williams *et al.* 2001).

2. METHODS

(a) Geographic ranges

Digital representations of ranges for 145 tree species were available online (<http://pubs.usgs.gov/pp/1999/p1650-a/>) from the United States Geological Survey and were imported into ARCVIEW GIS. I excluded 38 species whose ranges extend outside the continental United States and Canada into Greenland or

Table 1. Independent variables used in correlation and stepwise regression analyses, the hypotheses that they test and their correlation coefficients with range size.

hypotheses	independent variables	acronyms	r^c
CVH	largest value of annual temperature range (July maximum – January minimum normals) encompassed by a species' range (K)	T_{MAXRANGE}	0.844***
	largest value of annual precipitation range (highest monthly total – lowest monthly total; both normals) encompassed by a species' range (cm month ⁻¹)		-0.182
CEH	lowest January average daily minimum temperature encompassed by a species' range (K)	T_{MIN}	-0.885***
	highest July average daily minimum temperature encompassed by a species' range (K)		-0.057
	smallest annual total precipitation normal encompassed by a species' range; log transformed (cm yr ⁻¹)		-0.169
	smallest monthly total precipitation normal encompassed by a species' range; log transformed after adding one (due to zero values) (cm month ⁻¹)	P_{MIN}^b	0.223
OCH	largest monthly total precipitation normal encompassed by a species' range; log transformed (cm month ⁻¹)	P_{MAX}^b	-0.024
	average ^a annual mean temperature normals (K)	T_{AVG}^b	-0.620***
	average January minimum temperature normals (K)	T_{MINAVG}^b	-0.782***
	average July maximum temperature normals (K)		-0.131
	average annual temperature range: each station's maximum July temperature normals – minimum January temperature normals (K)		0.681***
	average total annual precipitation normals (cm yr ⁻¹)		-0.222
	average largest monthly total precipitation normals (cm month ⁻¹)	P_{MINAVG}	0.617***
	average smallest monthly total precipitation values (cm month ⁻¹)		-0.461***
	average within-year precipitation range: each station's largest monthly total precipitation – smallest monthly total precipitation, log transformed (cm)		-0.547***

^a The term 'average' used for all OCH variables refers here to the range-wide average calculated by using data from all climate stations encompassed by the given species' range.

^b Independent variables that are included in the full multiple regression (see § 3), but are excluded owing to strong multicollinearity.

^c *** $p < 0.001/15 = 0.000\ 07$ (Bonferroni-adjusted p values).

Mexico so as to maintain consistency in the quality and availability of climate and range data. There was no bias in the range sizes excluded, so it is unlikely that the results would be influenced in any systematic way. Four additional species were excluded because their extremely small ranges did not overlap sufficiently with climate station data (*Ostrya knowltonii*, *Cupressus backeri*, *Picea breweriana* and *Pinus aristata*). Finally, a total of 37 conifer and 66 hardwood species were used in the analyses (species list and additional data provided in electronic Appendix A, available on The Royal Society's Publications Web site). Within the GIS, species' ranges (which often consisted of multiple polygons; figure 1a inset) were overlaid onto a map of the continent in the Lambert equal area azimuthal projection. Range size for each species was calculated as the log of the proportion of the continental United States and Canada (corresponding to the area shown in figure 1) occupied by range pixels within binary equal-area maps. This is what 'range size' refers to hereafter.

(b) Climate data

Monthly climate normals for the period 1961–90 were acquired from weather stations throughout the continental United States (NOAA 1994) and Canada (Environment Canada 1994). A total of 5521 stations that provided both precipitation and temperature data for at least 20 years out of that period was used. 'Normals' refer to long-term averages, usually 30 years, but in this case 20 to 30 years. *Monthly* normals (used here) are

averages for the given month calculated over the long term. For example, the January daily minimum temperature normal for a given climate station represents the average January daily minimum temperature averaged over the 30 years. All encompassed stations were scanned to locate and extract the lowest and highest values of each climate normal (e.g. inset in figure 1a and caption), and the range-wide averages of the different temperature and precipitation normals were calculated for each range. All variables and their respective hypotheses are listed in table 1. I conducted a sensitivity analysis to ensure that mapping errors did not bias the results of these range and climate station overlap procedures and subsequent analyses. The procedures and results of this analysis are presented in electronic Appendix B. Annual temperature ranges were calculated as July daily maximum normals minus January daily minimum normals. For 748 of the 5521 stations (13.5%) February harboured the lowest monthly daily minimum normals as opposed to January, but the median difference in the temperature range values calculated the different ways was found to be only 0.33 (range: 0.055–3.1 K), so January daily minimums were used throughout for consistency.

(c) Statistical analyses

The degree of support for each hypothesis was initially evaluated by calculating Pearson correlation coefficients among the respective independent variables and range size (table 1). A forward stepwise multiple regression (probability of inclusion 0.05)

was then performed to determine which of the independent variables contributed significantly to explaining variation in range size. As is often the case with environmental data (Legendre & Legendre 1998), the predictor variables exhibited strong multicollinearity, so partial correlations and standardized regression coefficients were used to further monitor the sensitivity of the regression to multicollinearity. Where required, variables were transformed to achieve normality (table 1). Regression diagnostics were evaluated to ensure regression assumptions were met (Chambers & Hastie 1992). All statistical analyses (and randomization procedures in § 2d) were done by using the S-PLUS statistical software.

(d) *Accounting for phylogenetic and spatial non-independence*

Phylogenetic relatedness (Harvey & Pagel 1991) among the taxa used as well as spatial non-independence (Legendre & Legendre 1998) in the range and climate data have the potential to increase type-1 error rates and to bias probability values to higher significance (lower p values) than is warranted. I used randomization procedures to account for both potential sources of bias, with a form of spatial null model addressing the latter. The spatial null model also helped to minimize any effects arising from the uneven distribution of climate stations within the study region. The details of these procedures and their results can be found in electronic Appendix C.

3. RESULTS AND DISCUSSION

(a) *Relative support for hypotheses*

Although many variables were significantly correlated with range size (table 1), two in particular were remarkable: the largest value of annual temperature range encompassed by a species' range, T_{MAXRANGE} , and the lowest January average daily minimum temperature encompassed by a species' range, T_{MIN} . These relationships are predicted by CVH and the CEH, respectively. Not surprisingly, T_{MAXRANGE} and T_{MIN} were highly correlated with one another (Pearson's $r = -0.93$, $p < 0.001$). A standardized regression of T_{MAXRANGE} and T_{MIN} on range size revealed that the latter variable exhibited a much stronger direct effect ($\beta_{T_{\text{MAXRANGE}}} = 0.16$, $t = 1.31$; n.s.; $\beta_{T_{\text{MIN}}} = -0.73$, $t = -5.92$; $p < 0.001$) (Legendre & Legendre 1998). Thus, T_{MAXRANGE} was in fact correlated with range size mostly through its strong correlation with T_{MIN} .

A simple linear regression using T_{MIN} as the sole predictor accounted for 78% of the variation in range size ($F = 366.3$, $p < 0.001$; figure 3):

$$\text{range size} = 12.5927 - 0.0554 \times T_{\text{MIN}}.$$

Importantly, the relationship holds its form and strength across the latitudinal extent of the study area: within a follow-up regression, the northernmost latitudes of the species' ranges did not interact significantly with T_{MIN} ($p > 0.05$), and perhaps more telling, the slope of the above regression did not change significantly when the analysis was restricted to those species whose ranges lie entirely south of 48 °N ($n = 32$; $\beta_{T_{\text{MIN}}} = 0.0542$; significance of slope $p < 0.001$; test for difference in slopes $p > 0.1$). The breadth of range positions included in the dataset was substantial (northern extents: 36.02–70.31 °N; see electronic Appendix A).

Figure 3. The relationship between the lowest value of January average daily minimum temperature encompassed by a species' geographic range (T_{MIN}) and range size for hardwood shrub species (plus signs, $n = 37$), hardwood trees (inverted triangles, $n = 29$), conifer shrubs (open circles, $n = 4$), and conifer trees (closed circles, $n = 33$). Temperature is depicted here in Celsius (°C) for familiarity; add 273 to x-axis to achieve units in Kelvin, as used in regression analyses.

Equally important was that the relationship between range size and T_{MIN} was general for growth form (i.e. tree versus shrub, classified according to Gleason & Cronquist (1991)), conifers and hardwoods (figure 3). Using randomization procedures (Manly 1991), I found that the slopes for regressions done on the separate groups were indistinguishable from one another (conifer shrubs were not formally tested owing to low sample size, but they fall extremely close to the overall regression line; figure 3). Finally, the relationship between range size and T_{MIN} remained highly significant when taxonomic and spatial non-independence in the data were considered (electronic Appendix C).

A closer inspection of the single conifer tree species and single deciduous shrub species falling as outliers in the regression (near the -20 °C mark on the x-axis in figure 2) revealed the former to be *Picea pungens* (blue spruce) and the latter to be *Crataegus columbiana*, a hawthorn whose designation has changed recently (Phipps 1995, 1998). Removing the latter species increases the regression r^2 to 80.1%.

(b) *A possible mechanism underlying the effect of T_{MIN}*

Many factors are suspected of influencing the substantial breadth of range sizes (feature '(i)' in figure 2) found in a given continent (Brown 1995), so it is remarkable that a single variable, T_{MIN} , explains such a large proportion of the variation. The reason may lie in how T_{MIN} is related to interspecific variation in cold- and freezing tolerance. Cold climate has repeatedly been a strong selective force acting on the evolution of the flora of extra-tropical

regions (Sakai & Larcher 1987; Woodward 1987), and can thus be expected to be a dominant factor influencing range dynamics (Woodward 1990; Huntley 1991; Shafer *et al.* 2001) and, in turn, patterns of species richness (e.g. Latham & Ricklefs 1993; Currie 2001). The variety of range sizes exhibited by North American tree species could be a manifestation of the differential response of individual species to the low winter minimum temperatures currently typical of most of the continent (figure 1 caption; Woodward 1987).

To evaluate this hypothesis, I explored data about the freezing resistance of 35 of the species analysed here, published in Sakai & Weiser (1973) (electronic Appendix A). Interspecific variation in freezing resistance gains support as a contributory mechanism from two observations: (i) T_{MIN} is a good surrogate for temperatures at which freezing damage is first observed (Spearman $r = 0.75$, $p < 0.001$); and (ii) range size (as measured here) is strongly negatively correlated with those same critical temperatures (Spearman $r = -0.72$, $p < 0.001$).

(c) Multiple regression analysis

The full stepwise model (not shown) included five climate variables in addition to T_{MIN} (table 1) and accounted for 94% of the variation in range size, but the strong collinearity within and among temperature and precipitation variables rendered the model unstable and difficult to interpret. I therefore included only the next most important variable beyond T_{MIN} , as determined in the stepwise procedure. Six per cent of the variation in range size was explained over and above T_{MIN} with the addition of P_{MINAVG} (the range-wide average of the encompassed stations' lowest values of monthly total precipitation; $F = 259.98$, $r^2 = 0.84$, $p < 0.0001$): range size = $10.359 - 0.048(T_{\text{MIN}}) + 0.095(P_{\text{MINAVG}})$.

Standardized regression coefficients for T_{MIN} and P_{MINAVG} were -0.763 and 0.264 , respectively. P_{MINAVG} always entered second after T_{MIN} regardless of which, or how many intercorrelated variables were included in the stepwise procedure. In other words, it had the highest partial correlation with range size after controlling for T_{MIN} . It would be interesting to see if more complex measures of moisture availability, such as the ratio of actual to potential evapotranspiration (Huntley *et al.* 1995), would perform better than the straightforward precipitation measures used here. Although the role of moisture availability in governing forest types and species distributions is well understood (e.g. Stephenson 1998), how it relates to range size remains to be seen.

(d) Exploring the shape of the range-size distribution

It is useful to contemplate the ubiquitous right-skewed form of the range-size distribution (figure 2) in light of such a large proportion of the variation in range size explained by T_{MIN} . What constrains the maximum range sizes (feature '(ii)' in figure 2) attained by North American tree species? In part they are constrained by a certain proportion of the continent lacking the critical number of growing degree days and/or suitable edaphic conditions. But they may also be tempered by the fact that the widest-ranging, cold-tolerant (i.e. temperate/boreal) tree species cannot exist everywhere because they are generally

excluded from regions that are consistently warm and moist, such as the species-rich southeastern United States (Currie & Paquin 1987), owing to (i) the potential trade-off between cold tolerance strategies and competitive (in)ability in those warmer environments (e.g. Woodward 1987; Loehle 1998), and (ii) insufficiently cold temperatures for critical stages in their phenologies (e.g. Chuine & Beaubien 2001; Shafer *et al.* 2001). The lack of wide-ranging species (feature '(iii)' in figure 2), and in turn the wealth of species with small ranges (feature '(iv)' in figure 2) could perhaps each be attributable to historical factors (Ricklefs & Schluter 1993), considered together with the contemporary climate template of the continent: the significant and short-period oscillations (on evolutionary time-scales) in temperature experienced by much of North America north of Mexico since the Pliocene probably precluded speciation events, or precluded the persistence of any species that evolved cold tolerance during the relatively short and intermittent periods of 'stable' climate (Bennett 1990; Latham & Ricklefs 1993; McGlone 1996; Dynesius & Jansson 2000); hence relatively few species (Currie *et al.* 1999; Qian 1999) occupying the vast area of the continent that experiences freezing temperatures (figure 1b and caption). Meanwhile, a relatively small portion of the continental land area (e.g. the southeastern United States) currently harbours climate that is somewhat reminiscent of the flora's ancestral environments; hence the current, relative wealth of species with relatively small ranges occupying those regions (Qian 1999).

(e) Comparison with previous work

To evaluate the CEH and CVH in a way that truly reflected the mechanism that Stevens (1989) proposed, it was necessary to search the entire range of each species for the locations harbouring the most extreme values of all of the climate variables (e.g. T_{MIN} and T_{MAXRANGE}). In this way the spatially complex nature of the study region's climate (figure 1) was appropriately represented within the analyses. This is especially well illustrated by the fact that for 57 of the 103 species, different localities provided the T_{MIN} and T_{MAXRANGE} values (as shown for giant chinkapin, *Castanopsis chrysophylla*, in figure 1 inset). Other temperature and precipitation measures are less well intercorrelated, and were therefore provided from different localities even more frequently. This approach contrasts with previous evaluations of the CVH which used climate data extracted from central or latitudinal midpoint locations (e.g. Letcher & Harvey 1994; Ruggiero 1994; Cowlshaw & Hacker 1997; Harcourt 2000). I am unaware of any studies that have tested the CVH with respect to range size (as opposed to species richness; e.g. Kerr 1999) in a comparably 'spatially explicit' fashion. Revealing the true relationships between the various climate measures and range size is hindered without the use of such methods.

One assumption of the CVH for gradients in range size is that there also exist gradients in the physiological tolerances of species (Addo-Bediako *et al.* 2000). Evaluations of this assumption using insect taxa (see Gaston & Chown 1999a; Addo-Bediako *et al.* 2000) revealed that such gradients do exist, but that tolerance of cold temperatures is more important than tolerance of temperature variability. This latter finding has also been shown here. Geo-

graphical variation in the physiological ecology of tree species (and plants in general) is well understood (e.g. Saxe *et al.* 2001), and it has long been recognized that strategies for chilling and freezing tolerance are key features of temperate and boreal systems (Saxe *et al.* 2001). It may be that, given the limited extremes of *maximum* temperatures experienced by most extra-tropical regions, the geographic ranges of the resident tree species are, and have been, physiologically constrained more by critical minimum temperatures than by temperature variability *per se*.

As Stevens (1989) proposed the CVH as a possible explanation for *latitudinal* gradients in range size, an additional assumption was that there existed latitudinal gradients in the magnitudes of climatic variability (Addo-Bediako *et al.* 2000). The climate data used here demonstrate that this assumption is upheld in only the coarsest sense for North America north of Mexico (e.g. figure 1). More importantly, directionality in gradients are in fact not necessary for the proposed mechanism to apply, as evidenced by the findings presented here (figure 3).

(f) *Implications of climate change for species' ranges*

Almost all of North America north of Mexico currently experiences freezing temperatures (figure 1b). Indeed, only seven of the 103 species ranges analysed here did not include T_{MIN} values below freezing (figure 3). There is thus strong selective pressure on resident tree species to tolerate freezing conditions. Populations at range margins where temperatures are colder than the range-wide average may, over the long term and depending on the amount of genetic exchange from central regions of the range (Kirkpatrick & Barton 1997), adapt and allow range expansion into colder regions. However, given that it is the rapid warming of winter minimum temperatures that is driving current warming trends in North America (IPCC 2001), evolutionary processes are likely to be of secondary importance to current and imminent range dynamics in this continent (Huntley 1991). If minimum temperature does indeed exert the dominant constraint on range expansion for tree species in North America, then (all else being equal) the prediction is that tree species currently inhabiting restricted areas in warmer regions will be able to expand their ranges, leading to an 'evening-out' of the range-size distribution depicted in figure 2. There are obviously, however, many additional factors to consider, as discussed in recent modelling studies for North American tree species (e.g. Currie 2001; Iversen & Prasad 2001; Shafer *et al.* 2001).

I thank Brandon Schamp for suggesting Rapoport's rule as a topic for a course paper, Jeremy Kerr for raising the stakes at early stages, and Bob Thompson (and colleagues) at the US Geological Survey for providing the range data. Roly Tinline and Dave Ball of the Queen's University GIS laboratory provided assistance during early stages of the work. Lonnie Aarssen provided the logistical support to conduct the study, and insightful suggestions and comments along the way. Comments by Jim Austin, Stephen Bonser, Brian Cumming, Chris Eckert, Brian Enquist, Chris Herlihy, Rob Laird, Richard Pither, Phil Taylor, Janine Wiles, John Williams and three anonymous reviewers improved the manuscript. This study was conducted while I received funding from a Natural Sciences and Engineering Research Council of Canada post-

graduate scholarship, an Ontario Graduate Scholarship in Science and Technology, and from the Department of Biology at Queen's University.

REFERENCES

- Addo-Bediako, A., Chown, S. L. & Gaston, K. J. 2000 Thermal tolerance climatic variability and latitude. *Proc. R. Soc. Lond. B* **267**, 739–745. (DOI 10.1098/rspb.2000.1065.)
- Aizen, M. A. & Woodcock, H. 1996 Effects of acorn size on seedling survival and growth in *Quercus rubra* following simulated spring freeze. *Can. J. Bot.* **74**, 308–314.
- Barkley, T. M., Brouillet, L. & Spellenberg, R. W. (eds) 1993 *Flora of North America north of Mexico*, vol. 1. New York: Oxford University Press.
- Bell, G. 2001 Neutral macroecology. *Science* **293**, 2413–2418.
- Bennett, K. D. 1990 Milankovitch cycles and their effects on species in ecological and evolutionary time. *Palaobiology* **16**, 11–21.
- Brown, J. H. 1995 *Macroecology*. University of Chicago Press.
- Brown, J. H. 1999 Macroecology: progress and prospect. *Oikos* **87**, 3–14.
- Brown, J. H., Stevens, G. C. & Kaufman, D. M. 1996 The geographic range: size, shape, boundaries, and internal structure. *A. Rev. Ecol. Syst.* **27**, 597–623.
- Chambers, J. M. & Hastie, T. J. 1992 *Statistical models in S*. New York: Chapman & Hall (formerly Monterey: Wadsworth and Brooks/Cole).
- Chown, S. L. & Gaston, K. J. 1999 Exploring links between physiology and ecology at macro-scales: the role of respiratory metabolism in insects. *Biol. Rev. Camb. Phil. Soc.* **74**, 87–120.
- Chuine, I. & Beaubien, E. G. 2001 Phenology is a major determinant of tree species range. *Ecol. Lett.* **4**, 500–510.
- Cowlishaw, G. & Hacker, J. E. 1997 Distribution, diversity, and latitude in African primates. *Am. Nat.* **150**, 505–512.
- 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.
- Currie, D. J. & Paquin, V. 1987 Large-scale biogeographical patterns of species richness of trees. *Nature* **329**, 326–327.
- Currie, D. J., Francis, A. P. & Kerr, J. T. 1999 Some general propositions about the study of spatial patterns of species richness. *Ecoscience* **6**, 392–399.
- Dynesius, M. & Jansson, R. 2000 Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. *Proc. Natl Acad. Sci. USA* **97**, 9115–9120.
- Environment Canada 1994 *Canadian monthly climate data and 1961–1990 normals CD-ROM*. See http://www.msc-smc.gc.ca/climate/products_services/index_e.cfm.
- Farrell, B. D. & Mitter, C. 1993 Phylogenetic determinants of insect/plant community diversity. In *Species diversity in ecological communities: historical and geographical perspectives* (ed. R. E. Ricklefs & D. Schluter), pp. 253–266. University of Chicago Press.
- Gaston, K. J. 1994 *Rarity. Population and community biology series*. London: Chapman & Hall.
- Gaston, K. J. 1996 Species range-size distributions: patterns, mechanisms and implications. *Trends Ecol. Evol.* **11**, 197–201.
- Gaston, K. J. 1998 Species range-size distributions: products of speciation, extinction and transformation. *Phil. Trans. R. Soc. Lond. B* **28**, 219–230. (DOI 10.1098/rstb.1998.0204.)
- Gaston, K. J. 1999 A critique for macroecology. *Oikos* **84**, 353–368.
- Gaston, K. J. & Chown, S. L. 1999a Elevation and climatic tolerance: a test using dung beetles. *Oikos* **86**, 584–590.

- Gaston, K. J. & Chown, S. L. 1999b Why Rapoport's rule does not generalise. *Oikos* **84**, 309–312.
- Gaston, K. J. & He, F. 2002 The distribution of species range size: a stochastic process. *Proc. R. Soc. Lond. B* **269**, 1079–1086. (DOI 10.1098/rspb.2002.1969.)
- Gaston, K. J., Blackburn, T. M. & Spicer, J. I. 1998 Rapoport's rule: time for an epitaph? *Trends Ecol. Evol.* **13**, 70–74.
- Gleason, H. A. & Cronquist, A. 1991 *Manual of vascular plants of northeastern United States and adjacent Canada*, 2nd edn. New York: New York Botanical Garden.
- Harcourt, A. H. 2000 Latitude and latitudinal extent: a global analysis of the Rapoport effect in a tropical mammalian taxon: primates. *J. Biogeogr.* **27**, 1169–1182.
- Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. New York: Oxford University Press.
- Hill, J. K., Thomas, C. D. & Huntley, B. 1999 Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proc. R. Soc. Lond. B* **266**, 1197–1206. (DOI 10.1098/rspb.1999.0763.)
- Hughes, L., Cawsey, E. M. & Westoby, M. 1996 Geographic and climatic range sizes of Australian eucalypts and a test of Rapoport's rule. *Global Ecol. Biogeogr.* **5**, 128–142.
- Huntley, B. 1991 How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Ann. Bot.* **67**, 15–22.
- Huntley, B., Berry, P. M., Cramer, W. & McDonald, A. 1995 Modelling present and potential future ranges of some European higher plants using climate response surfaces. *J. Biogeogr.* **22**, 967–1001.
- IPCC 2001 *Climate change 2001: the scientific basis*. Cambridge University Press.
- Iverson, L. R. & Prasad, A. M. 2001 Potential changes in tree species richness and forest community types following climate change. *Ecosystems* **4**, 186–199.
- Kerr, J. T. 1999 Weak links: 'Rapoport's rule' and large-scale species richness patterns. *Global Ecol. Biogeogr.* **8**, 47–54.
- Kirkpatrick, M. & Barton, N. H. 1997 Evolution of a species' range. *Am. Nat.* **150**, 1–23.
- Latham, R. E. & Ricklefs, R. E. 1993 Continental comparisons of temperate-zone tree species diversity. In *Species diversity in ecological communities: historical and geographical perspectives* (ed. R. E. Ricklefs & D. Schluter), pp. 294–314. University of Chicago Press.
- Legendre, P. & Legendre, L. 1998 *Numerical ecology*. New York: Elsevier.
- Letcher, A. J. & Harvey, P. H. 1994 Variation in geographical range size among mammals of the palearctic. *Am. Nat.* **144**, 30–42.
- Little Jr, E. J. J. 1971 *Atlas of the United States trees. 1. Conifers and important hardwoods*, miscellaneous publication 1146. Washington, DC: US Department of Agriculture.
- Little Jr, E. J. J. 1976 *Atlas of the United States trees. 3. Minor western hardwoods*, miscellaneous publication 1314. Washington, DC: US Department of Agriculture.
- Little, E. J. J. 1977 *Atlas of the United States trees. 4. Minor eastern hardwoods*, miscellaneous publication 1142. Washington, DC: US Department of Agriculture.
- Loehle, C. 1998 Height growth rate trade-offs determine northern and southern range limits for trees. *J. Biogeogr.* **25**, 735–742.
- McGlone, M. S. 1996 When history matters: scale, time, climate and tree diversity. *Global Ecol. Biogeogr.* **5**, 309–314.
- Manly, B. F. J. 1991 *Randomization and Monte Carlo methods in biology*. New York: Chapman & Hall.
- NOAA 1994 *US divisional and station climatic data and normals*, vol. 1. US Department of Commerce. See <http://lwf.ncdc.noaa.gov/oa/ncdc.html>.
- Parker, J. 1963 Cold resistance in woody plants. *Bot. Rev.* **29**, 123–201.
- Phipps, J. B. 1995 The identity of *Crataegus columbiana* and its relationship to *C. piperi* (Rosaceae). *Taxon* **44**, 405–408.
- Phipps, J. B. 1998 Introduction to the red-fruited hawthorns (*Crataegus*, Rosaceae) of western North America. *Can. J. Bot.* **76**, 1863–1899.
- Qian, H. 1999 Spatial pattern of vascular plant diversity in North America north of Mexico and its floristic relationship with Eurasia. *Ann. Bot.* **83**, 271–283.
- Qian, H. & Ricklefs, R. E. 1999 A comparison of the taxonomic richness of vascular plants in China and the United States. *Am. Nat.* **154**, 160–181.
- Ricklefs, R. E. & Schluter, D. (eds) 1993 *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press.
- Rohde, K. 1999 Latitudinal gradients in species diversity and Rapoport's rule revisited: a review of recent work and what can parasites teach us about the causes of the gradients? *Ecography* **22**, 593–613.
- Rosenzweig, M. L. 1995 *Species diversity in space and time*. Cambridge University Press.
- Ruggiero, A. 1994 Latitudinal correlates of sizes of mammalian geographical ranges in South America. *J. Biogeogr.* **21**, 545–559.
- Sakai, A. & Larcher, W. 1987 *Frost survival of plants*. Berlin: Springer.
- Sakai, A. & Weiser, C. J. 1973 Freezing resistance of trees in North America with reference to tree regions. *Ecology* **54**, 118–126.
- Saxe, H., Cannell, M. G. R., Johnsen, B., Ryan, M. G. & Vourlitis, G. 2001 Tree and forest functioning in response to global warming. *New Phytol.* **149**, 369–399.
- Shafer, S. L., Bartlein, P. J. & Thompson, R. S. 2001 Potential changes in the distributions of western North America tree and shrub taxa under future climate scenarios. *Ecosystems* **4**, 200–215.
- Stephenson, N. L. 1998 Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. *J. Biogeogr.* **25**, 855–870.
- Stevens, G. C. 1989 The latitudinal gradient in geographic range: how so many species coexist in the tropics. *Am. Nat.* **133**, 240–256.
- Webb III, T. & Bartlein, P. J. 1992 Global changes during the last million years: climatic controls and biotic responses. *A. Rev. Ecol. Syst.* **23**, 141–173.
- Williams, J. W., Shuman, B. N. & Webb III, T. 2001 Dissimilarity analyses of late-quaternary vegetation and climate in eastern North America. *Ecology* **82**, 3346–3362.
- Woodward, F. I. 1987 *Climate and plant distribution*. Cambridge University Press.
- Woodward, F. I. 1990 The impact of low temperatures in controlling the geographical distribution of plants. *Phil. Trans. R. Soc. Lond. B* **326**, 585–593.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.

Visit <http://www.pubs.royalsoc.ac.uk> to see electronic appendices to this paper.