

1 **Late Quaternary climate stability and the origins and future of global grass endemism**

2 Original Article

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1 **Abstract**

2 *Background and Aims:* Earth's climate is dynamic, with strong glacial-interglacial cycles
3 through the Late Quaternary. These climate changes have had major consequences for the
4 distributions of species through time, and may have produced historical legacies in modern
5 ecological patterns. Unstable regions are expected to contain few endemic species, many species
6 with strong dispersal abilities and to be susceptible to the establishment of exotic species from
7 relatively stable regions. We test these hypotheses with a global dataset of grass species
8 distributions.

9 *Methods:* We described global patterns of endemism, variation in the potential for rapid
10 population spread, and exotic establishment in grasses. We then examined relationships of these
11 response variables to a suite of predictor variables describing the mean, seasonality and spatial
12 pattern of current climate and the temperature change velocity from the Last Glacial Maximum
13 to the present.

14 *Key Results:* Grass endemism is strongly concentrated in regions with historically stable
15 climates. It also depends on the spatial pattern of current climate, with many endemic species in
16 areas with regionally unusual climates. There was no association between the proportion of
17 annual species (representing potential population spread rates) and climate change velocity.
18 Rather, the proportion annual depended very strongly on current temperature. Among relatively
19 stable regions (less than 10 m/yr), increasing velocity decreased the proportion of species that
20 were exotic, but this pattern reversed for higher velocity regions (>10 m/yr). Exotic species were
21 most likely to originate from relatively stable regions with climates similar to those found in
22 their exotic range.

1 *Conclusions:* Long-term climate stability has important influences on global endemism patterns,
2 largely confirming previous work from other groups. Less well recognized is its role in
3 generating patterns of exotic species establishment. This result provides an important historical
4 context for the conjecture that climate change in the near future may promote species invasions.

5 **Keywords:** Poaceae, Grass, Endemism, Climate stability, Climate change velocity, Exotic
6 species, Climate change

1 **INTRODUCTION**

2 Over the last million years, Earth's climate has exhibited fairly regular cycles, with cold glacial
3 periods alternating with warm interglacials (Augustin *et al.*, 2004; Ruddiman, 2014). Species
4 distributions have shifted dramatically in response (Davis and Shaw 2001), but often lag behind
5 climate (Svenning and Skov 2007; Normand *et al.*, 2011; Ordonez, 2013; Sandel and Svenning,
6 2013; Svenning *et al.*, 2015). Understanding the consequences of this disequilibrium is crucial
7 for predicting ecosystem responses to anthropogenic change, and may be an important element
8 of understanding contemporary macroecological patterns (Sandel and Svenning, 2013; Svenning
9 *et al.*, 2015).

10 Evidence is accumulating that long-term climate stability can exert important influences
11 on species range sizes. This is expected because large ranges should reduce extinction risk
12 during climate cycles, while small climatic shifts make *in situ* survival more likely for small-
13 ranged species (Dynesius and Jansson, 2000). Thus, climatically stable areas are expected to
14 contain the largest concentrations of small-ranged species. This pattern has been observed
15 globally or regionally for birds, mammals, reptiles, amphibians and plants (Jansson 2003; Sandel
16 *et al.*, 2011; Morueta-Holme *et al.*, 2013; Feng *et al.*, 2016). With anthropogenic climate change
17 in the near future, many historically stable regions that contain many small-ranged species, such
18 as equatorial South America and Africa, are expected to experience large climate changes. Thus,
19 these areas represent a particular conservation concern (Sandel *et al.*, 2011).

20 While much attention has been given to the influence of climate stability on range size
21 patterns, other aspects of species distributions may also show important imprints of past climate.
22 For example, specialization is expected to decline with increasing climate instability because

1 constant range movement implies less time to adapt to local abiotic and biotic conditions
2 (Dynesius and Jansson, 2000). This has been tested in the context of species interaction
3 networks, with some studies showing effects of climate stability on network specialization
4 (Dalsgaard *et al.*, 2011) and modularity (Dalsgaard *et al.*, 2013), while others have found no
5 influence or effects opposite to expectation (Schleuning *et al.*, 2012, 2014; Sebastián-González
6 *et al.*, 2015). Historically unstable regions are also expected to contain more species with strong
7 dispersal ability (Dynesius and Jansson, 2000), as dispersal ability is a key trait influencing a
8 species' ability to track moving climate conditions. Consistent with this idea, flying ability has
9 been linked to persistence in unstable regions (Sandel *et al.*, 2011), and plant species with more
10 long-distance dispersal vectors are less strongly constrained to glacial refuges in Europe
11 (Normand *et al.*, 2011).

12 Long-term climate stability may also have important effects on community invasibility,
13 though this has not received much attention. As climate changes within a region, some resident
14 species will experience conditions further from their optimum (Blonder *et al.*, 2015). These
15 species may be replaced by immigrant species that are well-adapted to the new conditions.
16 However, if replacement is slowed by dispersal lags, the resident community may persist longer
17 than expected in a state of climate disequilibrium (Svenning and Sandel, 2013). Such a
18 community should be relatively open to invasion by new species, either nearby populations
19 overcoming their dispersal lags, or by exotic species introduced over greater distances by people.
20 Thus, we can predict that historically unstable regions may be more susceptible to exotic species
21 establishment, and that these exotic species will tend to come from relatively stable regions.

22 Taken together, then, historically unstable regions should contain few endemic species,
23 which are, on average, relatively unspecialized and strongly dispersing. These regions should

1 also contain the most exotic species. Empirical evidence for an effect of instability on endemism
2 is strong, while the other patterns are either more mixed (specialization) or hardly studied (exotic
3 species distributions).

4 Here, we focus on three specific hypotheses. First, we test the expected negative
5 relationship between climate instability and small-ranged species. Second, we ask whether
6 climatically unstable areas contain species with higher potential population spread rates. Third,
7 we ask whether climatically unstable areas contain more exotic species, which tend to come from
8 relatively stable areas. Finally, we compare past climate change velocities to those expected in
9 the future under climate change scenarios, [to determine which hotspots of endemism are likely to](#)
10 [remain climatically stable refugia in the near future](#). To test these predictions, we focus on the
11 grass family (Poaceae). The grasses are interesting in this context for several reasons. Much of
12 the work on climate stability and endemism is constrained to vertebrates, with less attention to
13 plants (but see Feng *et al.*, 2016). Grasses are an exceptionally diverse (>11,000 species),
14 ecologically and economically important family. Grass species have also been redistributed
15 globally by human activity, with grasses being unusually important invaders of both agricultural
16 and natural areas (Daehler, 1998). Thus, they provide an ideal group for understanding global
17 patterns of both native endemism and exotic species establishment.

18 **MATERIALS AND METHODS**

19 *Distributions*

20 Grass distributions were obtained from the World Checklist of Selected Plant Families at
21 Kew Royal Botanical Gardens (WCSP, 2015). This database provides species lists for TDWG
22 Level 3 units (Brummit, 2001), which correspond to countries or subnational units in large

1 countries such as states in the USA or provinces in Canada. In total, we used data for 11361
2 species from 369 political units. Hereafter, we refer to these units as “regions”.

3 For each region, we calculated two measures of endemism. First we calculated the
4 proportion of native species in the region that are found nowhere but that region (endemic
5 proportion, EP). For this measure, large regions are more likely to contain endemic species than
6 small ones. To address this bias, we also used a second approach. We calculated the range size of
7 each species as the summed area of the regions where it occurs, and defined any species with
8 range size $<750,000 \text{ km}^2$ as “small-ranged” (this cutoff was selected so that a single-region
9 endemic in most of the regions - 305 of 369 - would qualify as small-ranged). For each region,
10 we then calculated the proportion of native species that are small-ranged (small-ranged
11 proportion, SRP). Species occurring in regions $\geq 750,000 \text{ km}^2$ cannot be categorized as small-
12 ranged using this approach. This reverses the bias of the first approach, with small regions
13 becoming more likely to contain small-ranged species. In addition to considering these two
14 approaches with opposite biases, we also included region area as a predictor in regression
15 models. Consistent with the expected bias, region area had a positive influence on endemism
16 using the first definition, and a weak negative influence using the second definition (see results
17 for more details).

18 Population spread rates are a complex function of species traits, demographic parameters
19 and environmental characteristics. One particularly important indicator of spread rates is the age
20 at which a species reaches reproductive maturity (Nathan *et al.*, 2011). Early maturation
21 produces faster generation times, and allows higher population spread rates. We obtained
22 information on species lifespan (annual or perennial) from GrassBase (Clayton *et al.*, 2006
23 onwards; Vorontsova *et al.* 2015) for 97.6% of the species. We thereby operationalize the

1 hypothesis that climate instability should favor greater species spread rates by examining the
2 relationship between climate instability and the proportion of native species with annual life
3 histories (annual proportion, AP).

4 Finally, we considered patterns in the current distribution and origins of exotic grasses.
5 For each region, we calculated the proportion of grass species that are exotic (exotic proportion,
6 ExP).

7 Overall, we therefore calculated four response variables. Two relate to the hypothesis that
8 climatically stable areas should be a refuge for small-ranged species, with two different
9 definitions of small-ranged (EP and SRP). Another relates to the hypothesis that fast population
10 spread rates should be favored in unstable conditions, measured using the proportion of the
11 native species in a region that are annual (AP). Finally, we tested the hypothesis that unstable
12 regions should be more invasible using the proportion of species that are exotic in a region
13 (ExP).

14 *Predictor variables*

15 For each region, we calculated the average of several climate variables within that region,
16 based on Worldclim data (Hijmans *et al.*, 2005). We used four climatic variables describing the
17 average and seasonal variation in temperature and precipitation (mean annual temperature
18 (MAT), temperature seasonality (TS), mean annual precipitation (MAP) and precipitation
19 seasonality (PS)). MAT and TS were highly correlated, so TS was excluded from the regression
20 models described below.

21 In addition, we calculated a map of climate commonness. For each 0.25° grid cell in the
22 world, we calculated the proportion of surrounding cells within a 1000 km radius where MAT

1 was within 1 °C and MAP was within 100 mm of the focal cell. This approach is based on the
2 climate rarity measure of Ohlemüller *et al.* (2008) and detailed further in Sandel *et al.* (2011).
3 We call this variable the extent of analogous climate (EAC), and expect that areas with locally
4 unusual climates (low EAC values) will contain particularly many small-ranged or endemic
5 species. Following computation of these values on the 0.25° grid, values were averaged within
6 each region to obtain the final EAC variable.

7 Climate change velocity is a useful measure of climate instability that provides
8 ecologically-relevant units (distance/time). It describes the displacement rate of a particular
9 climate condition over Earth’s surface (Loarie *et al.*, 2009; Sandel *et al.*, 2011), and therefore
10 describes the minimum dispersal rate a population must attain to follow a particular climatic
11 condition. It is defined as the rate of climate change through time divided by the rate of change
12 over space. Thus, it represents two kinds of climate instability – steep temporal gradients and flat
13 spatial gradients. Here, we focus on climate change velocity from the Last Glacial Maximum
14 (21000 years ago) to the present. This glacial-interglacial transition is the most extreme such
15 transition in the Late Quaternary. However, the spatial pattern of warming in previous glacial-
16 interglacial transitions appears to be quite similar (Sandel *et al.*, 2011), though of somewhat
17 lesser magnitude. We calculated temperature change velocity over this interval, using the
18 approach described by Sandel *et al.* (2011), using two different LGM temperature map estimates
19 derived from the CCSM3 (Collins *et al.* 2006, Braconnot *et al.* 2006) and MIROC3.2 (K-1 model
20 developers 2004) models. The computation was performed at 2.5’ resolution; these values were
21 then averaged within each region. We call the resulting predictor variable “Velocity”.

22 Finally, we also calculated velocity estimates into the future. We used temperature
23 projections for the year 2080 under a moderate A1B emissions scenario, averaged across seven

1 climate models (CCCMA-CGCM31 [Canadian Centre for Climate Modelling and Analysis,
2 2010], CSIRO-MK30 [Gordon et al. 2003], IPSL-CM4 [Marti et al. 2010], MPI-ECHAM5
3 [Roeckner et al. 2003], NCAR-CCSM30 [Smith and Gent 2002], UKMO-HADCM3 [Johns et al.
4 2003] and UKMO-HADGEM1 [Johns et al. 2006]). We calculated the correlation of past and
5 expected future log velocities among regions. To identify endemism hotspots that might remain
6 relatively stable refugia in the future, we calculated a relative increase in velocity as the ratio of
7 expected future velocity to past velocity. Hotspots with $EP > 0.1$ and relatively small relative
8 velocity increases are potential refugia.

9 *Statistical analysis*

10 We began by fitting linear models to explain each of the four response variables from
11 MAT, MAP, PS, Velocity, EAC and the size of the region (Area). In one case, there was a clear
12 curved relationship between Velocity and ExP, so we added a quadratic term for Velocity in that
13 model. In all other cases, only linear terms were used, with no interactions between them (in
14 order to limit model complexity).

15 Models were fit using standard ordinary least squares (OLS) regression. However, this
16 produced spatially autocorrelated residuals, likely reflecting the omission of important unknown
17 predictor variables. To address this problem, we also fit error simultaneous autoregressive
18 models (`errorsarlm()` in the `spdep` package in R, Bivand *et al.*, 2013; Bivand and Piras, 2015)
19 with a 1000 km radius neighborhood and row standardization of the neighborhood weights
20 matrix. In addition, for each variable, we calculated the bivariate R^2 and the unique R^2 . The
21 bivariate R^2 is simply the squared correlation coefficient between the predictor and response
22 variable. The unique R^2 is calculated by fitting the full model and a model excluding the variable
23 of interest and computing the difference in R^2 values. Finally, we calculated an importance value

1 for each variable in each model as the summed Akaike weights of all models containing that
2 variable, using the MuMIn package in R (Barton, 2015).

3 Finally, we considered patterns in the origin of exotic species for each region in the
4 world. Treating each region in turn as the “focal” region, we took the set of exotic species from
5 that focal region, and calculated the species richness of these species in their native range. Thus,
6 for each non-focal region, we obtained the number of species that are native to that region and
7 exotic in the focal region. We then fit a linear model for each focal region to predict this
8 variation from Velocity and native species richness, along with the differences in climate
9 between each region and the focal region (see an example illustrated in Figure S1
10 [Supplementary Information]). We thereby obtained one model for each focal region. We
11 extracted standardized regression coefficients from these models and summarized them across
12 the whole model set with histograms. MAP, TS, PS, EAC and PA were square-root transformed
13 while Velocity, Area, EP, SRP were log transformed to improve linearity and normality of model
14 residuals. All analyses were performed in R 3.2.1 (R Core Team, 2015).

15

16 **RESULTS**

17 4354 (38%) grass species were single-region endemics, while 2818 (25%) were small ranged
18 (<750,000 km²). The spatial patterns of EP and SRP were positively correlated ($r = 0.636$), and
19 both exhibited fairly scattered spatial distributions with multiple hotspots (Figure 1). Velocity
20 was a negative predictor of both EP and SRP, and was the single most important predictor of
21 both, with the highest standardized regression coefficients, highest summed AIC weights and
22 highest unique R^2 (Table 1, Figure 2). EAC and PS were also particularly important negative

1 predictors of EP and SRP, while MAT was positively related to both. Region area had a strong
2 positive influence on EP and a weak negative influence on SRP.

3 The proportion of annual species was hardly associated with Velocity. Instead, it was
4 strongly influenced by current climatic conditions, primarily MAT (positive), MAP (negative)
5 and PS (positive) (Table 1, Figure 2).

6 The proportion of species that are exotic was most strongly influenced by EAC, PS and a
7 quadratic effect of climate change velocity (Table 1, Figure 2). Exotic species made up the
8 smallest proportion of species for intermediate velocity, low PS and low EAC values. Within
9 each region, exotic species were most likely to originate from species-rich regions with similar
10 MAT and low climate change velocity (Figure 3). With increasing Velocity of the focal region,
11 Velocity became an increasingly important negative predictor of species richness from the source
12 regions ($r = -0.349$, $P < 0.001$).

13 Velocities until 2080 are expected to be correlated with past velocities ($r = 0.824$), but of
14 much higher magnitude (Figure 4). Future velocities are expected to be between 40 and nearly
15 3000 times higher than past velocities (ranging from 29.5 m/yr to 4840 m/yr). The most stable
16 regions are predicted to experience velocities of around 30 m/yr a velocity which, considering
17 past changes, is associated with almost no endemic or small-ranged species (of the 56 regions
18 with past velocity > 30 m/yr, mean PE = 0.002 and mean PSR = 0.010). Among 55 regions with
19 EP at least 0.1 (endemism 'hotspots', Figure 4), velocity is expected to increase from an average
20 of 3.1 m/yr to 1090 m/yr. The endemism hotspots that are expected to experience the smallest
21 relative increases in velocity include some island regions, such as Macquarie Island, the
22 Antipodean Islands, Japan and the Azores. On the other hand, Hawaii is expected to experience

1 one of the largest relative increases in velocity (0.15 to 127 m/yr), potentially threatening the
2 many endemic species there (EP = 0.704). Among mainland endemism hotspots, parts of China,
3 Argentina and Turkey will remain relatively stable, while Ecuador, Venezuela and Morocco will
4 experience large increases in velocity.

5 **DISCUSSION**

6 Consistent with previous results (Jansson, 2003; Sandel *et al.*, 2011; Feng *et al.*, 2016), there was
7 a strong negative influence of climate change velocity on species endemism. In the most stable
8 regions, with climate change velocities of just a few cm/yr, the proportion of single-region
9 endemics reached about 0.1, and the proportion of small-ranged species about 0.5. In contrast,
10 the most unstable regions, with velocities up to 100 m/yr, had almost no endemic or small-
11 ranged species. This suggests that regions with stable Late Quaternary climates have had either
12 or both of higher rates of new endemic species formation and lower rates of extinction.

13 Climate change velocity had almost no influence on the proportion of species with annual
14 life histories. There are several possible explanations for this. First, it is possible that velocity
15 and potential population spread rates are in fact unrelated in grasses. Second, while there are
16 good reasons to expect the annual life history to be related to high spread rates, it may be too
17 rough an indicator (Clark *et al.* 2003). Finally, the proportion of species that are annuals appears
18 to be strongly influenced by current climate, including temperature, precipitation and
19 precipitation seasonality. Strong selection by current climate conditions may leave little residual
20 variation that could be explained by long-term climate stability. Unfortunately, quantifying
21 population spread rates across large groups of species is very challenging, and we are often
22 limited to coarse indicators. However, a study of population spread found rates for grasses

1 typically less than 1 m/yr (Brunet and Von Oheimb, 1998), which is less than the climate
2 velocity in all but 9% of regions. Though based on a limited sample size, these rates are
3 comparable to values for other herbaceous species (Matlack, 1994; Brunet and Von Oheimb,
4 1998; Bossuyt *et al.*, 1999). Thus, climate change velocities are large compared to known
5 capacities for spread, suggesting that variation in spread rates should have important
6 consequences for survival in climatically unstable regions, even if the annual/perennial
7 distinction is insufficient to capture this variation.

8 Though a number of studies have suggested that future climate change may increase the
9 invasibility of communities (e.g. Stachowicz *et al.*, 2002; Hellmann *et al.*, 2008; Bradley *et al.*
10 2010), to our knowledge no study has assessed the impact of previous climate fluctuations on
11 invasibility. Here, we show that past climate change velocity is related to the proportion of
12 species that are exotic in a region, though not [linearly](#). For moderate to large velocities (roughly
13 >8 m/yr), we observed the expected increase in the exotic proportion with increasing velocity.
14 However, for lower velocities, the proportion of exotic species actually declined with increasing
15 velocity.

16 Historically stable regions are the primary sources for exotic species, particularly for
17 focal regions with historically unstable climates. This may reflect something like a large-scale
18 competition-colonization tradeoff (Turnbull *et al.*, 2004). In unstable regions, species may have
19 to invest more in dispersal (e.g. produce more and smaller seeds) in order to track climate
20 changes. This may be less advantageous in stable regions, favoring instead investment in traits
21 related to competition (e.g. tall stature and large seeds). In California, for example, the exotic
22 grasses are indeed taller and larger-seeded than the natives that they frequently outcompete
23 (Sandel and Dangremond, 2012). This result contrasts somewhat with a recent analysis of cross-

1 continental patterns in donors and recipients of exotic vascular plant species (van Kleunen *et al.*,
2 2015). There, the dominant pattern was that the Northern Hemisphere is the source of species
3 that naturalize in the Southern Hemisphere, which may be due in part to the relative isolation of
4 the Southern Hemisphere continents making them more island-like, despite the fact that they
5 have also experienced more stable climates.

6 If general, this result may have important implications for invasive risk assessment. Our
7 results agree with previous work indicating the climate matching, particularly with respect to
8 temperature, is an important determinant of exotic species transfer (e.g. Wiens and Graham,
9 2005; Mahoney *et al.*, 2015). An important general role of climate stability would help target
10 exotic monitoring efforts where there are highest risks.

11 *Climate change and the future of endemism*

12 In the next 65 years, Earth's regions are expected to experience temperature velocities
13 that are 40 to nearly 3000 times higher than those since the LGM, with minimum velocities
14 around 30 m/yr. This gives a worrying picture of the future prospects for endemic species. If
15 endemic and small-ranged species have survived previous climate changes primarily in areas
16 with low velocity (around 1-10 m/yr), there is reason to think that they might not survive
17 upcoming climate changes with much higher rates.

18 However, the magnitudes of climate change velocity from the LGM to present represent a
19 long-term average rate, which masks dramatic variation within that period. For example, North
20 America experienced median temperature velocities of 254 m/yr from about 14,000 to 12,000
21 years ago (Ordonez, 2013), which is within the range of expected rates in the near future (though
22 on the low end). With even finer temporal resolution, more extreme climate shifts become ever

1 more apparent. The most dramatic of these, the Younger Dryas event, ending about 11,700 years
2 ago, included a 7° C warming in Greenland over 50 years (Dansgaard *et al.*, 1989), with
3 evidence for an even more abrupt transition in snow accumulation occurring over just a few
4 years (Alley *et al.*, 1993). A more moderate, but similarly rapid, transition also occurred in the
5 Cariaco Basin off of Venezuela, where the termination of the Younger Dryas brought an increase
6 of more than 3° C (Lea *et al.*, 2003). These changes produced local and short-term velocities that
7 were several thousand times higher than the long-term average.

8 Thus, the velocities expected in the near future may have some near precedents in the
9 historical record, at least in certain periods. Species survival at a site is likely to be a function of
10 both the velocity and duration of climate change. Very high velocities may be survivable if they
11 last only a decade, while even low velocities may be problematic if sustained over millennia. An
12 important element, therefore, is the expected duration of anthropogenic climate change. While
13 much planning and forecasting concerns the next century or so, atmospheric CO₂ levels are
14 expected to be elevated until at least the year 3000, with corresponding temperature changes up
15 to about 4° C (Plattner *et al.* 2008). Still, in this period, this would produce velocities not much
16 higher than were observed in the deglaciation around 14,000 to 12,000 years ago.

17 However, it is important to note that, while the expected velocities do have some recent
18 historical precedent, other aspects of anthropogenic climate change do not. Atmospheric CO₂,
19 N₂O and CH₄ concentrations are higher than they have been for at least 800,000 years and
20 temperatures will likely exceed the range experienced in this period (Masson-Delmotte *et al.*,
21 2013).

1 Some regions with high endemism will be exposed to relatively low velocities in the near
2 future; these may become particularly important conservation targets. Many of these regions are
3 topographically heterogeneous islands, which provide a high capacity to buffer species from
4 change. At the same time, though, these regions also tend to have large numbers of exotic
5 species, presenting a different potential threat to the native endemic grasses. Hawaii is a
6 particularly concerning case, with very high endemism, a large number of exotic species, and
7 particularly large expected relative increases in future velocity.

8 *Conclusion*

9 Historical climate changes have left strong imprints on global endemism patterns in the grasses.
10 In addition, long-term climate stability is an important predictor of both the degree of exotic
11 species establishment and the sources of exotic species. Both results have important implications
12 for predicting impacts of anthropogenic climate change, and suggest large extinction threats to
13 endemic species and likely increases in exotic species establishment world-wide.

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9

10 **FIGURE CAPTIONS**

11 Figure 1: Maps of the four response variables: (a) endemic proportion (EP), (b) small-ranged
12 proportion (SRP), (c) annual proportion (AP), and (d) exotic proportion (ExP).

13 Figure 2: Bivariate relationships between the four response variables and the three
14 most important predictor variables for each (according to AIC weights). Lines show
15 fitted lowess curves.

16 Figure 3: Histograms of regression coefficients describing variation in exotic species
17 sources. For each region, a regression was fit to explain global variation in species
18 richness of species exotic to that focal region, as a function of (a)-(d) the difference
19 between each region and the focal region in MAT, MAP, TS and PS, (e) the climate
20 change velocity and (f) the native richness of the countries. White portions of each
21 histogram indicate non-significant ($P > 0.05$) regression coefficients. The number of

1 regions with positive or negative regression coefficients is indicated in each histogram,
2 and the number of significant regression coefficients is reported in brackets.

3 Figure 4: Past climate change velocity (a), expected future velocity (b) and the ratio of
4 expected future:past (c, relative velocity increases). In each map, the 55 regions with
5 $EP > 0.1$ (endemism hotspots) are outlined.

6

1 Table 1: Summary of predictor variable influence on four response variables: endemic proportion
 2 (EP), small-ranged proportion (SRP), annual proportion (AP) and exotic proportion (ExP). OLS
 3 and SAR give standardized regression coefficients from OLS and SAR models, respectively. P
 4 values are displayed as: ***, $P < 0.001$; **, $P < 0.01$; and *, $P < 0.05$. Importance indicates the
 5 summed AIC weights of all models containing the variable (the three most important variables in
 6 each case [excluding Area] are in bold and plotted in Figure 2), Bivar. R^2 gives the squared
 7 correlation coefficient between the predictor and response variable, and Unique R^2 the portion of
 8 the full model R^2 that is uniquely attributable to that predictor. R^2 values for SAR models are
 9 Nagelkerke's pseudo- R^2 .

| EP | OLS | SAR | Importance | Bivar. R^2 | Unique R^2 |
|------------|-----------|-----------|--------------|--------------|--------------|
| MAT | 0.101 | 0.187** | 0.466 | 0.011 | 0.006 |
| MAP | -0.075 | -0.134 | 0.325 | 0.011 | 0.003 |
| PS | -0.185** | -0.145 | 0.884 | 0.011 | 0.017 |
| Velocity | -0.522*** | -0.428*** | 1.000 | 0.178 | 0.138 |
| EAC | -0.205* | -0.213* | 0.875 | 0.057 | 0.014 |
| Area | 0.473*** | 0.438*** | 1.000 | 0.007 | 0.111 |
| Full R^2 | 0.291 | 0.363 | | | |
| SRP | | | | | |
| MAT | 0.066 | 0.06 | 0.508 | 0.035 | 0.002 |
| MAP | -0.006 | -0.005 | 0.280 | 0.123 | 0.000 |
| PS | -0.202*** | -0.127 | 0.995 | 0.028 | 0.020 |
| Velocity | -0.353*** | -0.287*** | 1.000 | 0.272 | 0.063 |
| EAC | -0.263*** | -0.306*** | 0.999 | 0.337 | 0.023 |
| Area | -0.102 | -0.104 | 0.728 | 0.229 | 0.005 |
| Full R^2 | 0.429 | 0.476 | | | |
| AP | | | | | |
| MAT | 0.705*** | 0.694*** | 1.000 | 0.470 | 0.282 |
| MAP | -0.222*** | -0.152** | 1.000 | 0.005 | 0.023 |
| PS | 0.164*** | 0.232*** | 0.989 | 0.236 | 0.013 |
| Velocity | -0.055 | -0.075 | 0.410 | 0.039 | 0.002 |
| EAC | 0.172** | 0.085 | 0.872 | 0.004 | 0.010 |
| Area | -0.108* | -0.063 | 0.784 | 0.005 | 0.006 |
| Full R^2 | 0.608 | 0.773 | | | |
| ExP | | | | | |
| MAT | 0.127** | 0.203*** | 0.902 | 0.000 | 0.009 |
| MAP | -0.055 | -0.061 | 0.369 | 0.123 | 0.001 |

| | | | | | |
|-----------------------|-----------|-----------|--------------|-------|-------|
| PS | -0.38*** | -0.351*** | 1.000 | 0.321 | 0.071 |
| Velocity | 0.128** | 0.12* | 0.910 | 0.008 | 0.008 |
| Velocity ² | 0.223*** | 0.139*** | 1.000 | 0.197 | 0.039 |
| EAC | -0.28*** | -0.26*** | 1.000 | 0.221 | 0.025 |
| Area | -0.304*** | -0.256*** | 1.000 | 0.377 | 0.042 |
| Full R ² | 0.604 | 0.676 | | | |

1