# Climate-induced range overlap among closely related species

**Meade Krosby[1,2]\*, Chad B. Wilsey[3†], Jenny L. McGuire[3†], Jennifer M. Duggan[3†], Theresa M. Nogeire[3],
Julie A. Heinrichs[3], Joshua J. Tewksbury[1,4] and Joshua J. Lawler[3]**

**Contemporary climate change is causing large shifts in biotic
distributions[1], which has the potential to bring previously
isolated, closely related species into contact[2]. This has led
to concern that hybridization and competition could threaten
species persistence[3]. Here, we use bioclimatic models to show
that future range overlap by the end of the century is predicted
for only 6.4% of isolated, congeneric species pairs of New
World birds, mammals and amphibians. Projected rates of
climate-induced overlap are higher for birds (11.6%) than for
mammals (4.4%) or amphibians (3.6%). As many species will
have difficulty tracking shifting climates[4], actual rates of future
overlap are likely to be far lower, suggesting that hybridization
and competition impacts may be relatively modest.**

Widespread changes in species distributions due to climate
change are documented for diverse taxa and are expected to become
more pronounced over the coming century as rates of warming
increase[1]. One expected outcome of climate change-induced range
shifts is the establishment of geographic range overlap among
previously isolated taxa, leading to novel species interactions
and assemblages[5,6]. The potential for climate change to result in
new interactions among closely related species has given rise to
conservation concern, as these may have negative consequences
for species persistence. Climate-induced range contact between
ecologically similar species may introduce high levels of inter-
specific competition to populations already stressed by changing
climatic conditions[7,8]. In addition, recently diverged species
with incomplete reproductive barriers may hybridize, reducing
population fitness through genetic admixture or leading to species
extinctions through asymmetric hybridization[9,10]. Although few
studies have empirically documented climate-induced contact
among closely related species[2], many have expressed concern
that it could lead to a significant loss of biodiversity[3,11].

Despite potential for negative impacts, no attempt has yet been
made to estimate future rates of climate-induced geographic overlap
among previously isolated, closely related species. We used biocli-
matic models to predict potential end-of-century (2071–2100) areas
of climatic suitability for 9,577 congeneric species pairs, including
New World birds ($n = 3,858$), mammals ($n = 1,661$) and amphibians
($n = 4,058$). From this data set, we calculated the number of non-
overlapping (that is, allopatric), congeneric species pairs with ranges
projected to come into contact (that is, sympatry) in the coming
century. We accounted for variability among estimates by including
in our results only species pairs projected to come into contact under
a majority (>5) of 10 general circulation models (GCMs).

We found that 6.4% of 4,796 allopatric species pairs are projected
to come into geographic contact by the end of the century (Fig. 1).
Rates of future contact for species pairs were significantly greater
for birds than mammals or amphibians (generalized linear mixed
model, $F_{1,4781} = 8.54, P < 0.0002$), for tropical than temperate species
($F_{1,4781} = 5.21, P < 0.0055$), and increased with current geographic
range size ($F_{1,478} = 11.55, P < 0.0007$).

Our finding that future range overlap is more than twice as
common for bird species pairs (11.6%) than mammals (4.4%) or
amphibians (3.6%) cannot be explained by higher dispersal rates
in birds, as our models assume equal dispersal capacities across
taxa. Rather, it is best explained by the larger range sizes of birds
(analysis of variance (ANOVA), $F_{2,402} = 9.897, P < 0.001$) and the
positive relationship between current range size and rate of future
overlap (Fig. 2).

For most newly overlapping species, projected areas of future
overlap span a relatively small (<25%) percentage of their future
bioclimatic envelope (Fig. 3). However, this percentage is negatively
correlated with the size of a species' future bioclimatic envelope
($R^2 = 0.358$, d.f. $= 1,614, P < 0.001$; Fig. 4), which is itself highly cor-
related with current range size ($R^2 = 0.543$, d.f. $= 1,614, P < 0.001$).
Thus, species with smaller ranges, now and in the future, may have
the greatest potential for negative impacts, because higher propor-
tions of their future ranges are expected to overlap with that of a
congener, and because smaller-ranged species are particularly vul-
nerable to the negative effects of overlap with closely related species[9].

Our finding that most areas of future overlap are in the tropics
(85.8%) can be explained by current species distributions (Fig. 1):
86.2% of species pairs include a tropical species. Additionally, future
bioclimatic envelopes of pairs that include tropical species are
projected to have greater overlap (ANOVA, $F_{2,305} = 3.231, P = 0.041$;
Table 1) and size asymmetry (ANOVA, $F_{2,305} = 27.220, P < 0.001$;
Table 1) than pairs with only temperate species, both of which
may exacerbate the potential for negative impacts[9]. Thus, both the
occurrence and impact of climate-induced range overlap between
closely related species may be greatest in the tropics.

As newly overlapping species do not overlap in current climate
space, future areas of overlap must be interpreted as having
no-analogue climates. Caution must be used when extrapolating
future species distributions from no-analogue future climates
because it is difficult to predict how species will respond to new
environments[5,12]. Thus, although our results may estimate the
proportion of species pairs that are likely to come into geographic
contact (that is, parapatry), whether species are able to occupy

[1]Department of Biology, University of Washington, Box 351800, Seattle, Washington 98195-1800, USA. [2]Climate Impacts Group, University of
Washington, Box 355674, Seattle, Washington 98195-5674, USA. [3]School of Environmental and Forest Sciences, University of Washington, Box 352100,
Seattle, Washington 98195-2100, USA. [4]Luc Hoffman Institute, WWF International, Avenue du Mont-Blanc, 1196 Gland, Switzerland. [†]Present addresses:
National Audubon Society, 220 Montgomery Street, Suite 1000, San Francisco, California 94104-3402, USA (C.B.W.); Georgia Institute of Technology,
School of Biology, 310 Ferst Drive, Atlanta, Georgia 30332, USA (J.L.M.); Division of Science and Environmental Policy California State University, Monterey
Bay 100 Campus Center Seaside, California 93955-8000, USA (J.M.D.). \*e-mail: mkrosby@uw.edu
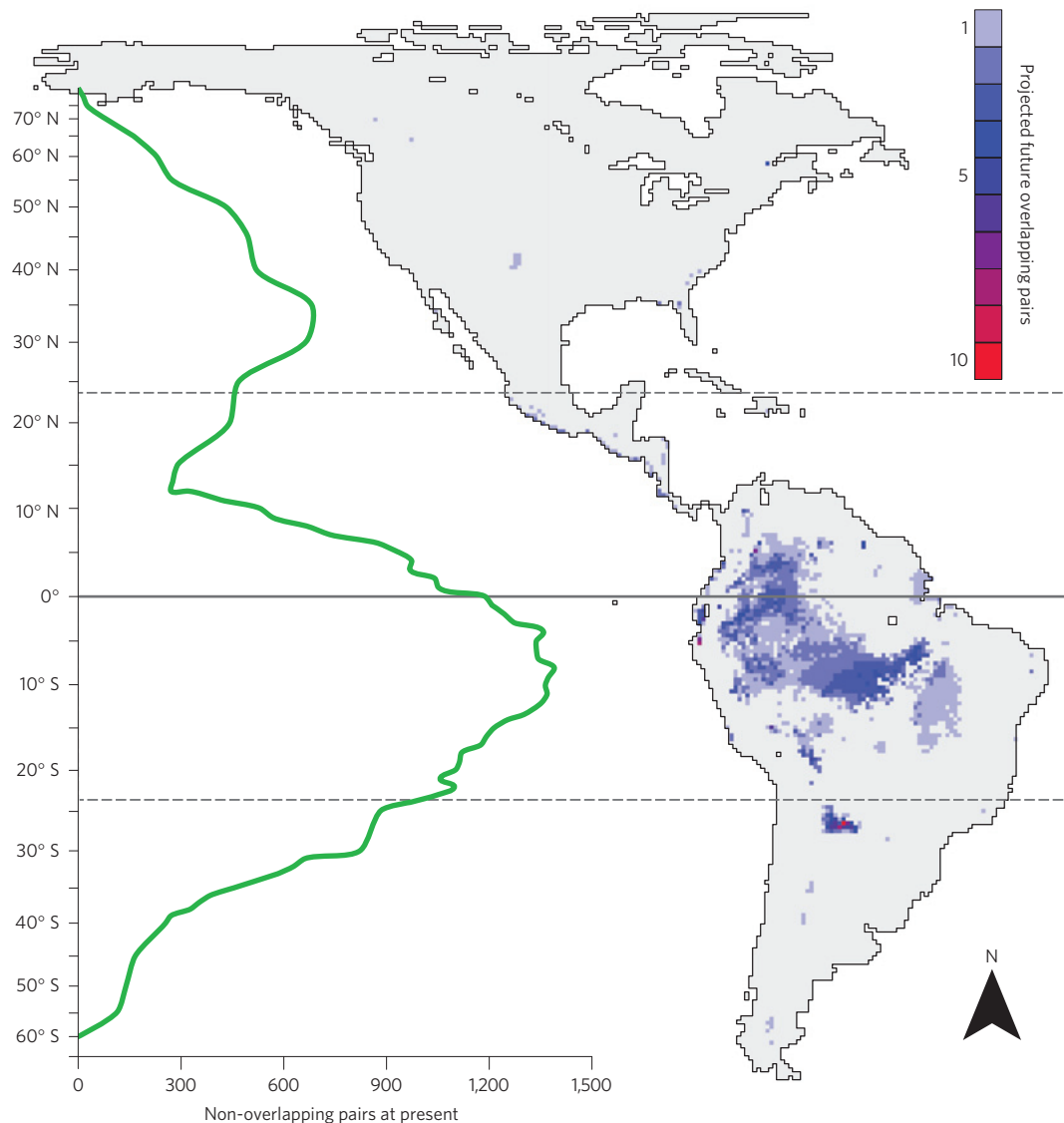
**Figure 1 | Projected future overlap for isolated, congeneric species of New World birds, mammals and amphibians.** Coloured cells in map indicate areas where new overlap among species pairs is predicted by >5 of 10 GCMs; grey cells indicate areas where a majority of GCMs do not predict new overlap. The green line shows the number of non-overlapping species pairs at present, by latitude.

projected areas of range overlap and achieve coexistence (that is, sympatry) will depend on their abilities to persist in novel climates.

However, species interactions are likely to be even more important than climate in determining whether species are able to realize projected areas of overlap. Indeed, use of bioclimatic models to predict climate-induced range shifts has been criticized for ignoring the role of species interactions in shaping species range limits[13,14]. Thus, although these bioclimatic models clearly show where potential for future range overlap of closely related species is relatively high (for example, the Amazon basin), realized future rates of range overlap are likely to be lower. This is because closely related species are likely to interact in ways that prevent co-occurrence.

On secondary contact, closely related species are likely to compete for common resources and/or hybridize, both of which may prevent sympatry[15]. Closely related, ecologically similar species are expected to experience high rates of inter-specific competition[16], so that, in the absence of character displacement, competitive exclusion often prevents co-occurrence[7,8]. Incomplete reproductive isolation among recently diverged species may also

prevent sympatry if hybrid zone formation hinders further range expansion and overlap[17], or if asymmetric hybridization leads to the loss of one of the species[9]. In some cases, hybridization may benefit populations and facilitate range shifts by increasing genetic diversity and adaptation potential[18].

Our study represents a first attempt to estimate the frequency with which climate change may bring isolated, closely related species into geographic contact. As our analysis includes only congeneric species pairs, future studies estimating rates of future overlap for intra-specific populations, subspecies or species between the congener and family level would greatly improve understanding of this relatively unstudied biological impact of climate change. In addition, future studies based on mechanistic models, which incorporate important biotic determinants of range shifts (for example, species interactions; vegetation effects; and *in situ* evolutionary, epigenetic or plastic adaptations), may provide more accurate estimates of future overlap than our bioclimatic approach. Our ability to anticipate consequences of new overlap would be improved by additional empirical studies of climate-induced
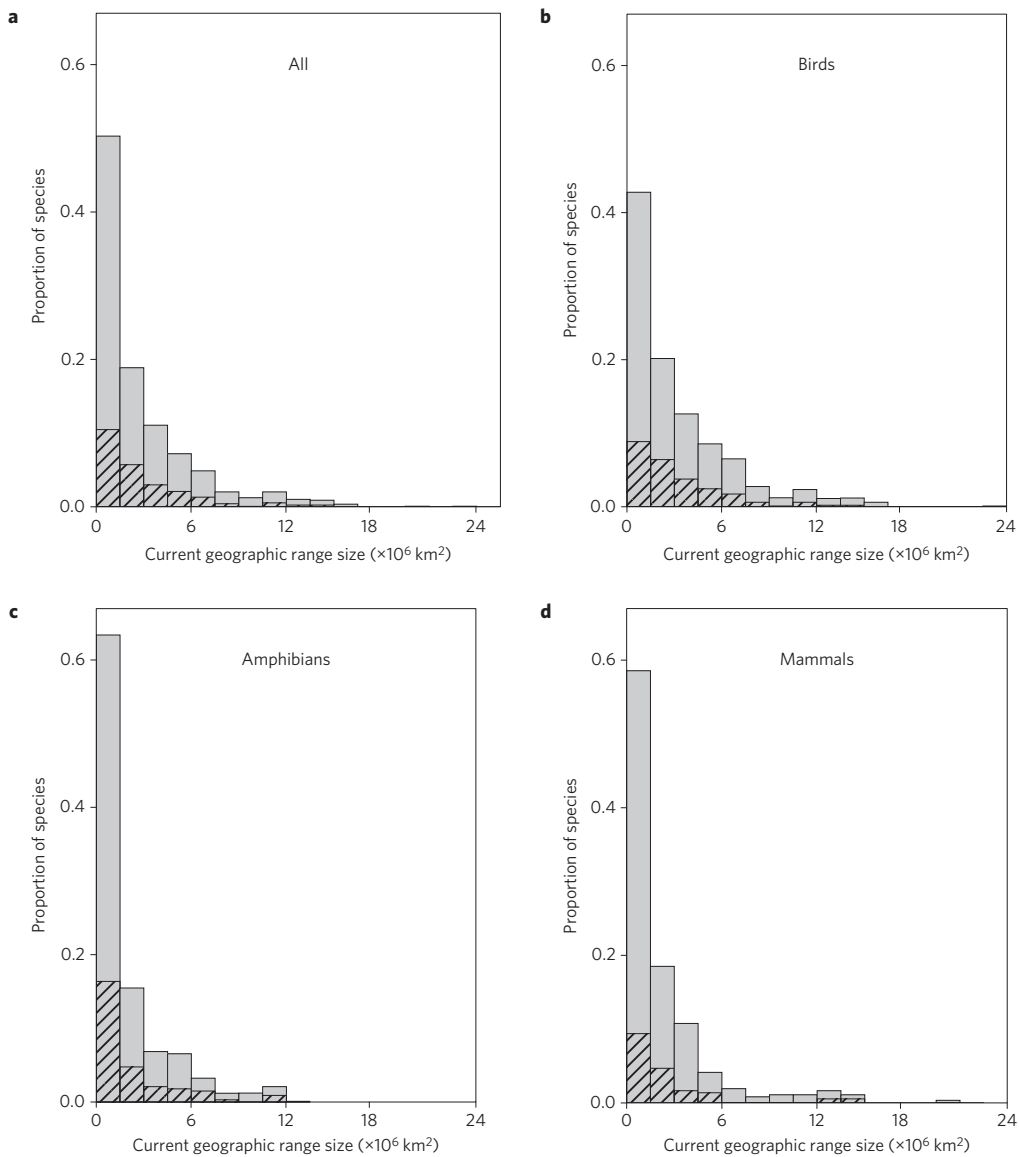
**Figure 2 | Current geographic range size and proportion of future range in overlap. a–d**, Current geographic range sizes of non-overlapping species (grey bars), and the proportion of each range size class projected to come into future geographic contact with an isolated congener (hashed bars) for all taxa (**a**), birds (**b**), amphibians (**c**) and mammals (**d**).

range overlap, which will require rigorous, widespread monitoring of species ranges and interactions; closely related taxa in close proximity present obvious targets for such efforts. Our ability to predict novel species assemblages will also require better modelling approaches for no-analogue communities and more research into their appropriate interpretation and application.

Ultimately, however, limited dispersal abilities and significant anthropogenic barriers to movement will prevent many species from successfully tracking climate to potential areas of future overlap[4,19]. The high probability that species ranges will be unable to track shifting areas of climatic suitability across increasingly fragmented habitats has made landscape connectivity enhancement the leading climate adaptation strategy for biodiversity conservation[20]. Our results suggest that there is little reason for concern that efforts to increase connectivity could have the unintended consequence of bringing previously isolated taxa into contact[21]. Even if species were perfectly able to track shifting climates, our results predict that the number of species that may come into climate-driven overlap with a congener, is likely to be dwarfed by the number of species that are likely to be unable to find suitable climate space by the 2050s[4,22], and,
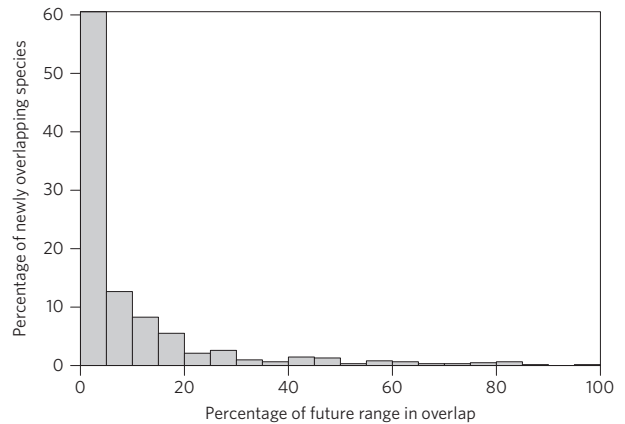


**Figure 3 | The percentage of a species' future bioclimatic envelope projected to overlap with that of an isolated congener.** Individual species may be represented more than once, as several species are projected to come into future overlap with more than one congener.

**Table 1 | Mean degree of future overlap and mean future range size asymmetry for isolated species pairs projected to come into future contact, for pairs that at present contain 0, 1 or 2 tropical species.**

| Number of tropical species in a species pair | Mean degree of future overlap* | Mean future range size asymmetry† |
|---|---|---|
| 0 | 0.08 | 4.52 |
| 1 | 0.07 | 10.39 |
| 2 | 0.18 | 14.00 |

*We calculated degree of future overlap as the sum of the projected future bioclimatic envelopes of both species in a pair divided by the future bioclimatic envelope of the species with the smaller future bioclimatic envelope[23]. Overlap values can range from 0 (when future bioclimatic envelopes do not overlap), to 1 (when the smaller bioclimatic envelope falls entirely within the larger or when ranges of equal size completely overlap). †We calculated future range asymmetry as the size of the larger future bioclimatic envelope divided by the size of the smaller future bioclimatic envelope[23].
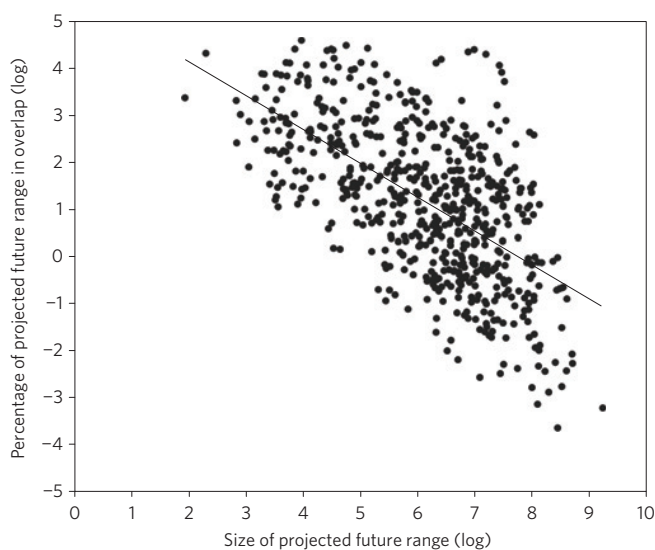


**Figure 4 | The percentage of future range in overlap as a function of future range size.** This is calculated as the percentage of each species' ($s_i$) future bioclimatic envelope projected to overlap with a currently isolated congener ($s_j$), as a function of the future bioclimatic envelope size of $s_i$. The trend line represents a linear regression model ($R^2 = 0.358$, d.f. $= 1,614$, $P < 0.001$).

indeed, by the number that are likely to be brought into contact by other human activities[9]. Thus, the benefit of increasing connectivity as a means of mitigating climate-driven biodiversity losses is likely to outweigh the relatively small risk that it might lead to hybridization and competition among closely related species.

## Methods
Methods and any associated references are available in the online version of the paper.

## References
1. Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B. & Thomas, C. D. Rapid range shifts of species associated with high levels of climate warming. *Science* **333,** 1024–1026 (2011).
2. Chunco, A. Hybridization in a warmer world. *Ecol. Evol.* **4,** 2019–2031 (2014).
3. Kelly, B. P., Whiteley, A. & Tallmon, D. The arctic melting pot. *Nature* **468,** 891 (2010).
4. Schloss, C. A., Nunez, T. A. & Lawler, J. J. Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proc. Natl Acad. Sci. USA* **109,** 8606–8611 (2012).
5. Williams, J. W. & Jackson, S. T. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* **5,** 475–482 (2007).
6. Walther, G. R. *et al.* Ecological responses to recent climate change. *Nature* **416,** 389–395 (2002).
7. Jankowski, J. E., Robinson, S. K. & Levey, D. J. Squeezed at the top: Interspecific aggression may constrain elevational ranges in tropical birds. *Ecology* **91,** 1877–1884 (2010).
8. Urban, M. C., Tewksbury, J. J. & Sheldon, K. S. On a collision course: Competition and dispersal differences create no-analogue communities and cause extinctions during climate change. *Proc. R. Soc. B* **279,** 2072–2080 (2012).
9. Rhymer, J. M. & Simberloff, D. Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* **27,** 83–109 (1996).
10. Beatty, G. E., Philipp, M. & Provan, J. Unidirectional hybridization at a species' range boundary: Implications for habitat tracking. *Divers. Distrib.* **16,** 1–9 (2010).
11. Mallet, J., Wynne, I. R. & Thomas, C. D. Hybridisation and climate change: Brown argus butterflies in Britain (Polyommatus subgenus Aricia). *Insect Conserv. Divers.* **4,** 192–199 (2011).
12. Fitzpatrick, M. C. & Hargrove, W. W. The projection of species distribution models and the problem of non-analog climate. *Biodivers. Conserv.* **18,** 2255–2261 (2009).
13. Araújo, M. B. & Luoto, M. The importance of biotic interactions for modelling species distributions under climate change. *Glob. Ecol. Biogeogr.* **16,** 743–753 (2007).
14. Hellman, J. J., Prior, K. M. & Pelini, S. L. The influence of species interactions on geographic range change under climate change. *Ann. NY Acad. Sci.* **1249,** 18–28 (2012).
15. Vallin, N., Rice, A. M., Arntsen, H., Kulma, K. & Qvarnström, A. Combined effects of interspecific competition and hybridization impede local coexistence of Ficedula flycatchers. *Evol. Ecol.* **26,** 927–942 (2012).
16. Burns, J. H. & Strauss, S. Y. More closely related species are more ecologically similar in an experimental test. *Proc. Natl Acad. Sci. USA* **108,** 5302–5307 (2011).
17. Barton, N. H. & Hewitt, G. M. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* **16,** 113–148 (1985).
18. Becker, M. *et al.* Hybridization may facilitate *in situ* survival of endemic species through periods of climate change. *Nature Clim. Change* **3,** 1039–1043 (2013).
19. Theobald, D. M., Reed, S. E., Fields, K. & Soule, M. Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. *Conserv. Lett.* **5,** 123–133 (2012).
20. Heller, N. E. & Zavaleta, E. S. Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biol. Conserv.* **142,** 14–32 (2009).
21. Hilty, J. A., Lidicker, W. Z. Jr & Merenlender, A. *Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation* (Island Press, 2006).
22. Thomas, C. D. *et al.* Extinction risk from climate change. *Nature* **427,** 145–148 (2004).
23. Anacker, B. L. & Strauss, S. Y. The geography and ecology of plant speciation: Range overlap and niche divergence in sister species. *Proc. R. Soc. B* **281,** 20132980 (2014).

## Author contributions
M.K. conceived the study. M.K., C.B.W., J.M.D., J.L.M., J.A.H., T.M.N., J.J.T. and J.J.L. designed the analysis. C.B.W. and J.M.D. conducted most of the data analysis, with additional analysis completed by J.L.M., T.M.N., J.A.H. and M.K. M.K., J.J.L., J.J.T., C.B.W. and J.M.D. wrote the paper.

## Methods

To estimate future overlap of currently isolated congeneric species, we used previously published bioclimatic models built for 2,954 New World birds ($n = 1,818$), mammals ($n = 723$) and amphibians ($n = 413$; ref. 24). Bioclimatic models relate species' current distributions to historical climate. These models are then used to project the distribution of suitable climates into the future on the basis of output from global climate models. The models were built in R using random forest classifiers[25,26]. Although other modelling approaches could potentially provide different projections of future climatic suitability, we used an approach that proved to be more accurate at projecting current ranges when compared with five other approaches applied to a subset of the species used in the present study[27]. For each species, presences and absences were modelled as a function of current climate. Species distribution data were taken from digital range maps for birds[28], mammals[29] and amphibians (data available on-line, http://www.globalamphibians.org). Species ranges were mapped to a 50-km grid. Both current and future climatic conditions were represented by 37 bioclimatic variables (Supplementary Table 1). These included both annual and seasonal variables, and basic climate variables (for example, temperature and precipitation) as well as derived variables (for example, a moisture index and growing degree days). To represent current climatic conditions, historical climate data were downscaled from the University of East Anglia Climatic Research Unit's (CRU's) CL 1.0 (ref. 30), CL 2.0 (ref. 31) and TS 2.1 (ref. 32) climate data sets to the 50-km by 50-km grid using locally weighted, lapse-rate-adjusted interpolation. The current climate was represented by averaged climatic variables over a 30-year period (1961–1990). Future climate data were taken from 10 general circulation model (GCM) simulations archived by the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3). These climate projections were averaged over a 30-year period from 2071 to 2100 and represent climates simulated for a mid-to-high (SRES A2) greenhouse gas emissions scenario[33]. Models included in this analysis had a mean accuracy rate of 99% for absences and 92% for presences in a subset of locations not used during model construction. For a more detailed description of the modelling approach, see ref. 24.

We measured the prevalence of current range overlap for 9,577 congeneric species pairs (note that many species have multiple congeners), including 3,858 avian, 1,661 mammalian and 4,058 amphibian species pairs. Ranges included only breeding distributions for migratory species. Congener status was determined on the basis of shared genus names in 2009. We estimated end-of-century (2071–2100) areas of suitable climate for each species on the basis of projected climate from 10 GCMs using the A2 greenhouse gas emissions scenario, which represents the mid-to-high range of the scenarios described in the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios[33] (SRES). We then calculated the number of non-overlapping species pairs whose projected future distributions overlap. We used model agreement among 6 or more of the 10 GCMs as a cutoff for determining which species pairs are projected to come into contact by the end of the century.

We used a generalized linear mixed model (GLIMMIX procedure, SAS University Edition; SAS Institute) to test whether current geographic range size,

taxonomic class (birds, mammals and amphibians), or the number of species classified as tropical in a species pair (neither, one, or both species with $>50\%$ geographic range between latitudes $-25°$ and $25°$), as well as interactions between these factors, significantly influenced the occurrence of future overlap of species pairs. The GLIMMIX procedure models normal and non-normal data with correlated responses. We used a binomial distribution and logit link function for the response variable (overlap versus non-overlap). As most species had multiple congeners and therefore occurred in multiple species pairs, we included species as an R-side (residual) effect, and we modelled the covariance structure using variance components. An R-side effect is equivalent to a repeated measures effect, but the GLIMMIX procedure does not provide type III (analysis of variance) estimates for variance components. Thus, we accounted for within-subject correlations in our analysis, but we did not test for the significance of species. We estimated degrees of freedom for $F$-tests using the Kenward–Roger method to suppress inflation of type 1 error[34]. Additionally, we used analyses of variance to evaluate differences in current range size among taxa and to test whether the degree of future range overlap and asymmetry increases with the number of tropical species in a pair. Finally, we used linear regressions to examine relationships between current geographic range size and proportion of future range in overlap, and between current and future geographic range size. We used a natural log transformation of all range size and overlap data, as distributions of these variables were right-skewed[23].

## References

24. Lawler, J. J. *et al.* Projected climate-induced faunal change in the Western Hemisphere. *Ecology* **90,** 588–597 (2009).
25. Breiman, L. Random forests. *Mach. Learn.* **45,** 5–32 (2001).
26. R Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2009); http://www.R-project.org
27. Lawler, J. J., White, D., Neilson, R. P. & Blaustein, A. R. Predicting climate-induced range shifts: Model differences and model reliability. *Glob. Change Biol.* **12,** 1568–1584 (2006).
28. Ridgely, R. S. *et al. Digital Distribution Maps of the Birds of the Western Hemisphere* (NatureServe, 2003).
29. Patterson, B. D. *et al. Digital Distribution Maps of the Mammals of the Western Hemisphere* (NatureServe, 2007).
30. New, M., Hulme, M. & Jones, P. Representing twentieth-century space-time climate variability. Part I: Development of a 1961–90 mean monthly terrestrial climatology. *J. Clim.* **12,** 829–856 (1999).
31. New, M. *et al.* A high-resolution data set of surface climate over global land areas. *Clim. Res.* **21,** 1–25 (2002).
32. Mitchell, T. D. & Jones, P. D. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.* **25,** 693–712 (2005).
33. Nakicenovic, N. *et al. Special Report on Emissions Scenarios* (IPCC, Cambridge Univ. Press, 2000).
34. Kenward, M. G. & Roger, J. H. Small sample inference for fixed effects from restricted maximum likelihood. *Biometrics* **53,** 983–997 (1997).