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SYNTHESIS

Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change

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ABSTRACT

Aim The factors that set species range limits underlie many patterns in ecology, evolution, biogeography and conservation. These factors have been the subject of several reviews, but there has been no systematic review of the causes of warm-edge limits (low elevations and latitudes). Understanding these causes is urgent, given that the factors that set these limits might also drive extinction at warm edges as global climate changes. Many authors have suggested that warm-edge limits are set by biotic factors (particularly competition) whereas others have stressed abiotic factors (particularly temperature). We synthesize the known causes of species' warm-edge range limits, with emphasis on the underlying mechanisms (proximate causes).

Location Global.

Methods We systematically searched the literature for studies testing the causes of warm-edge range limits.

Results We found 125 studies that address the causes of warm-edge limits, from a search including > 4000 studies. Among the species in these studies, abiotic factors are supported more often than biotic factors in setting species range limits at warm edges, in contrast to the widely held view that biotic factors are more important. Studies that test both types of factors support abiotic factors significantly more frequently. In addition, only 23 studies (61 species) identified proximate causes of these limits, and these overwhelmingly support physiological tolerances to abiotic factors (primarily temperature). Only eight species with identified proximate causes were tested for both biotic and abiotic factors, but the majority support abiotic factors.

Main conclusions Although it is often assumed that warm-edge limits are set by biotic factors, our review shows that abiotic factors are supported more often among the species in these 125 studies. However, few studies both identify proximate causes and test alternative mechanisms, or examine the interaction between biotic and abiotic factors. Filling these gaps should be a high priority as warm-edge populations are increasingly driven to extinction by climate change.

Keywords

Biotic interactions, climate change, competition, physiological tolerances, range limits, temperature.

INTRODUCTION

Many patterns in ecology, evolution and conservation are related to the geographical distribution of species. In turn, these distributions depend on the factors that set species range limits. Given this, understanding the causes of species range limits (e.g. Gaston, 2003; Parmesan *et al.*, 2005; Sexton *et al.*, 2009) is a fundamental issue for many fields. For

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example, the factors setting species range limits have been shown to be important in explaining latitudinal and elevational patterns of species richness (e.g. Wiens *et al.*, 2006; Kozak & Wiens, 2010; Giehl & Jarenkow, 2012), patterns of community structure (e.g. Stephens & Wiens, 2009; Savage & Cavender-Bares, 2012), the spread of invasive species (e.g. Peterson, 2003; Broennimann *et al.*, 2007; Alexander & Edwards, 2010), and allopatric speciation (e.g. Kozak & Wiens, 2006; Peterson & Nyári, 2007).

Different factors may set the limits of different parts of the range of a single species (reviewed in Brown *et al.*, 1996). The factors that set the warm-edge limits are especially interesting and important. We define warm-edge range limits as the latitudinal and elevational edges of a species' range closest to the equator and at the species' lower elevational limits (thus potentially warmer, but not necessarily determined by temperature).

On one level, warm-edge limits are intrinsically enigmatic. Species richness in most clades is maximized towards the equator (reviewed in Hillebrand, 2004) and richness is often especially high in the lowland tropics. Climatic conditions therefore seem relatively benign and non-stressful for many groups in the tropics and the potential for interspecific interactions may be higher due to higher richness (Dobzhansky, 1950; Kaufman, 1995). Based on these ideas, some authors have suggested that biotic factors should become more important towards the equator, and in turn that warm-edge limits are set by biotic factors rather than by limited tolerances to climatic conditions (e.g. Dobzhansky, 1950; MacArthur, 1972; Kaufman, 1995). The importance of biotic interactions to warm-edge range limits has since become widely assumed without being rigorously tested (see also Hampe & Jump, 2011), and despite many potential complicating factors (e.g. whether the warm-edge occurs within tropical or temperate regions and latitudinal and elevational variation in seasonality and precipitation). The major alternative hypothesis is that abiotic conditions are intolerable for the species at warm-edge range limits (e.g. Jones *et al.*, 2009, 2010; Somero, 2012). This might imply that evolving to tolerate conditions in colder, low-richness regions comes with a loss of tolerance to warmer conditions, possibly reflecting limits to the breadth of a species' thermal tolerance (reviewed in Angilletta, 2009). Furthermore, despite the general trend for high richness at low latitudes and elevations, many clades show higher richness in higher latitudes (e.g. Janzen, 1981; Smith *et al.*, 2005; Buckley *et al.*, 2010a) or at mid-elevations (e.g. Rahbek, 1995, 1997; McCain, 2005, 2007, 2009; Smith *et al.*, 2007; Wiens *et al.*, 2007; Li *et al.*, 2009; Kozak & Wiens, 2010). Thus, the factors that set warm-edge limits are also key to explaining many important biodiversity patterns.

On another level, understanding the factors that set warm-edge range limits is also a potentially important conservation issue. Many species are shifting their geographical ranges seemingly in response to recent climate change, and these shifts are typically upward in elevation and poleward in latitude (e.g. Parmesan & Yohe, 2003; Hickling *et al.*, 2005; Parmesan, 2006; Anderson *et al.*, 2009; Thomas, 2010; Chen *et al.*, 2011; but see Lenoir *et al.*, 2010). These shifts may involve both expansion at the species' cool range edge (high latitude, high elevation) and range contractions at the warm edge. Range contractions suggest that species are undergoing local extinction at these warm edges, especially for sessile organisms (e.g. Hickling *et al.*, 2005; Perry *et al.*, 2005; Parmesan, 2006; Jones *et al.*, 2009, 2010, 2012; Thomas, 2010; Chen *et al.*, 2011; Wethey *et al.*, 2011). These local extinctions may represent a latitudinal or elevational shift in the factors that naturally set the species' warm-edge range limits. Thus, these factors may become the direct causes of population extinctions as climate changes, and effectively predicting and ameliorating the impacts of climate change may depend on knowing these factors (Parmesan *et al.*, 2005; Sunday *et al.*, 2012). However, to evaluate whether these factors are indeed the same, we need to identify the factors that set these warm-edge limits.

Several recent reviews have examined the causes of species range limits (e.g. Parmesan *et al.*, 2005; Gaston, 2009; Sexton *et al.*, 2009), but none focused specifically on the warm edge. Parmesan *et al.* (2005) synthesized 145 studies of range edges, but their search for studies was not systematic (i.e. using replicable automated searches of literature databases with specified keywords; Pullin & Stewart, 2006; Lowry *et al.*, 2012). Gaston (2009) focused on demographic causes of range limits (e.g. how birth and death rates change at range edges), but not limiting factors or warm edges. Sexton *et al.* (2009) systematically reviewed 146 studies on the causes of range limits, but did not focus on warm edges. Thus, despite many empirical studies on species range limits, warm-edge limits have not been the focus of any previous reviews and so general conclusions about their causes cannot be drawn.

Additionally, the proximate causes of these limits are often unknown. We define the proximate cause as the specific factor(s) that prevent establishment of populations outside the current range of the species. These proximate causes include limited physiological tolerances to specific abiotic factors (e.g. high maximum summer temperatures, low soil pH), along with many potential biotic factors, including the abundance of species with negative impacts (e.g. competitors, predators and parasites) and scarcity of species that provide necessary resources (e.g. microhabitats, food and pollination). We use the term 'proximate cause' to emphasize that range limits along climatic gradients must have a specific explanation beyond climate itself, even in cases where spatial change in climate is the ultimate, underlying cause of the range limit (for analogous use for climate change see Cahill *et al.*, 2013).

The importance of proximate causes is exemplified by temperature. Temperature is often cited as a factor determining warm-edge limits, but without identifying a specific proximate cause, it is not clear what this means. 'Temperature' may refer to limited physiological tolerance to high temperature (e.g. Jones *et al.*, 2009, 2010), temperature-mediated competition or other biotic interactions (e.g. Wethey, 2002), or it may simply mean that the range limit is statistically associated with higher values of a temperature-related climatic variable based on species distribution modelling, and the specific cause is unknown. We argue that a full understanding of species range limits is only possible if we know these proximate causes.

Here, we synthesize information on the causes of warm-edge range limits by conducting a systematic review of published empirical studies. We focus on the relative importance of abiotic and biotic factors, as well as proximate causes. To our knowledge, this is the first systematic review on warm-edge limits.

MATERIALS AND METHODS

We conducted two searches in the ISI Web of Science database on 7 June 2012. First, we repeated the search of Sexton *et al.* (2009) on causes of range limits. Keywords in this first search were 'geographic range limit,' 'geographic range boundary,' 'geographic distribution limit,' and 'geographic distribution boundary.' In our second search we included various synonyms for 'geographic' and 'boundary' (from Gaston, 2003) and included keywords to select for studies involving causative mechanisms. The full keyword search was: [(species (range or distribution) (border* or boundar* or edge* or limit* or margin*)) AND (biogeograph* or geograph* or global or altitud* or elevation*)] AND (caus* or determin*).

Merging results from the two searches yielded 4259 unique records. Abstracts were screened and papers clearly unrelated to warm-edge range margins were discarded. We excluded many studies on beta diversity and community assembly that did not explicitly examine range limits. We also eliminated studies of geographical barriers to dispersal (e.g. rivers for terrestrial species), which are presumably unrelated to warm edges per se. We excluded studies that only measured demographic parameters at range edges because we were interested in the mechanisms controlling these parameters, not the parameters themselves. We excluded review papers to avoid double-counting case studies. The 629 remaining studies were reviewed in depth and many additional studies were discarded based on the criteria above, leaving 125 relevant studies (see Appendix S1 in Supporting Information).

We first classified the range-limiting factors examined in these studies into 11 categories: (1) temperature; (2) precipitation (including soil moisture); (3) other soil variables (e.g. soil type, pH); (4) other abiotic factors; (5) competition; (6) predation/herbivory; (7) host/food availability; (8) parasitism/disease; (9) other biotic factors; (10) interactions between abiotic and biotic factors (e.g. temperature-dependent competition); and (11) physiological tolerances (i.e. studies that used laboratory or field measures of tolerance to temperature, desiccation and other factors). Note that a study testing 'physiological tolerances' would also be scored as testing an abiotic factor that was the subject of the physiological test. However, a study could be classified as testing an abiotic factor without specifying a 'physiological tolerance' (i.e. no physiological tests were conducted, but see below on proximate causes). For each study, we noted whether each factor examined was supported, based on the conclusions of the authors. Like other studies of this type, we did not attempt to further verify or reanalyse the results presented in these studies.

We then classified studies using the following guidelines (see Appendix S1): A = an association was found between one or more limiting factors and the warm-edge range limit and the underlying mechanism (proximate cause) was verified; B = an association with a potentially limiting factor was found, and a mechanism was suggested but not verified; C = an association with a potentially limiting factor was found, but no mechanism was suggested; and D = no association was found between the factors investigated and the warm-edge range limit. We first examined results across all studies (A–D) and then focused on those that identified proximate causes (A). We recognize that these categories are potentially somewhat subjective, but our results should be largely insensitive to their use due to our focus on proximate causes.

We then grouped the methods used into three categories: experiments (laboratory and field), observations and models (Appendix S1). Note that a single study could fall into multiple categories (i.e. use multiple methods), and there is considerable heterogeneity within these broad categories. Many studies used more than one method to test the causes of species range limits (mean = 1.18 methods per study), although many also used only one general approach. Only one study used methods from all three categories (experiments, observations and models). Studies in category C (association was found with a range limit, but a mechanism was only speculated) were generally modelling studies, but all classes of methods were used in studies from all four categories of studies (A–D).

Many studies examined multiple species, but few analysed > 10. When analysing our data, we summarized results on a per-species basis for studies of 1–10 species and on a per-study basis for studies of 11 or more (studies of > 10 species tended to focus only on abiotic factors; see Results). Species that appeared more than once in our database were counted each time they appeared: nine species appeared twice in the database and one species (*Fagus sylvatica*) appeared five times. The factors causing range limits may vary in time or space (even for warm edges), and different studies of the same species can detect these nuances. In addition, multiple studies of the same species may widen the range of factors examined. A potential exception is studies of the same species by the same researchers in the same location; such studies were combined (three cases). Studies of > 10 species were counted such that any factor related to the warm-edge limit examined and supported in the study applied to the study as a whole (e.g. if one species had its warm-edge limit set by competition and 10 others by temperature, the study was counted as supporting both factors). Species that appear multiple times in studies using > 10 species are unlikely to influence the results because grouping the data by study downweights the importance of any one species.

We did not use meta-analysis techniques in analysing our results because most studies we reviewed did not present data that would allow us to quantify the level of support (i.e. effect size) for any given hypothesis concerning the cause of warm-edge range limits, as required for meta-analysis (Gurevitch & Hedges, 2001). Indeed, a meta-analysis is not the best approach for the questions that we address here because we are interested in which factors do or do not set warm-edge range limits, and what is the general pattern among species, not in how strongly one factor is supported across studies. Instead, we emphasize the generality of the patterns that we find, including across species, gradients (latitude versus elevation), major clades (plants versus animals), and environments (marine versus terrestrial; tropical versus temperate). However, we acknowledge that our inferences are based largely on the conclusions of the original authors, rather than reanalysis of their data or other quantitative assessments of the strength of their conclusions. We note that some might consider our approach similar to 'vote counting' among studies, an approach often criticized relative to meta-analysis. These criticisms emphasize low statistical power as the primary problem of vote counting (e.g. Harrison, 2011; Koricheva & Gurevitch, 2013). However, given that we do find statistically significant results (see Results), this issue does not invalidate our conclusions.

We conducted three types of statistical analyses. First, we calculated the correlation between the factors examined and supported using the 11 categories of factors as units of analysis and species as data points (i.e. were factors usually supported in the species in which they were studied). We used the 178 species from studies of ≤ 10 species and Kendall's τ due to non-normality of the data (Kolmogorov–Smirnov test, $P < 0.001$). Second, we estimated standard errors for proportions using the formula: standard error = $\sqrt{(\text{estimate} \times (1 - \text{estimate})/n)}$, where 'estimate' is the proportion as calculated from our data and n is the sample size of species (Gelman & Hill, 2007). Third, to test for significant support for a greater prevalence of abiotic versus biotic factors among species studied for both, we conducted a G-test of association in species found to support one type of factor or the other ($n = 26$ species). All statistical analyses were conducted in R 3.0.1 (R Core Team, 2013) and BIOMstat 3.3 (Rohlf & Slice, 2008).

The earliest paper to meet our inclusion criteria was published in 1985 (Appendix S1), and some potentially relevant papers were therefore not included (e.g. Heller, 1971). This may be an artefact of using the ISI database (many studies prior to 1990 are not included). Furthermore, we are aware of some recent studies that our ISI search did not find, but which nevertheless contain analyses of the causes of warm-edge range limits. However, we restricted our analysis to those studies found by our explicit, repeatable search (rather than deviating from this protocol to include other studies, which we could not guarantee to be unbiased in their selection). Although it is possible to modify our search terms and potentially find more studies, we found that such modifications generated thousands of clearly irrelevant studies (e.g. excluding caus* or determin* generates > 11,000 studies, of which relatively few appear relevant). Overall, our survey yielded a number of warm-edge studies similar to the total number of studies in other recent reviews including all types of range limits (see Introduction). Thus, it seems likely that our findings should be consistent with what would be found given a truly exhaustive sampling of the literature.

RESULTS

Our search identified 125 studies that addressed the causes of warm-edge range limits (see Appendix S1 for references and other details), including 105 studies of ≤ 10 species and 20 studies of > 10 species. The studies of ≤ 10 species include a total of 178 species. Among these 178 species, most live in terrestrial habitats ($n = 120$), with fewer in marine ($n = 48$) and freshwater ($n = 10$) systems. These species spanned a range of higher taxa (1 protozoan, 114 plants/algae, 63 metazoans). Most species were studied at their latitudinal limits ($n = 112$), with fewer at elevational limits ($n = 48$) or both ($n = 18$). Most species were studied in North America ($n = 79$) and Europe ($n = 66$), although all seven continents are represented. Among the 125 studies, 73 studies used a modelling approach, 71 used observations from the field, and 89 used experimentation in the laboratory or field; many studies used multiple approaches.

Results reported hereafter are specifically from the set of 178 species (Fig. 1), but are similar for the 20 studies of > 10 species (Fig. 2, Appendix S1). Few studies of > 10 species tested biotic factors ($n = 4$ out of 20), and only two of those studies found any support for biotic factors. Many different factors were both tested and supported among the 178 species (Fig. 1), and there is a strong correlation between factors examined and factors supported (Kendall's $\tau = 0.934$, $P < 0.001$). Abiotic factors were supported for 79.2 ± 3.2% of 164 species examined compared with 59.2 ± 7.0% (among 49 species examined) for biotic factors. Among abiotic factors, both temperature (68.8 ± 3.7%, $n = 157$ species tested), and precipitation (56.6 ± 5.4%, $n = 83$ species tested) were frequently supported. Among biotic factors, predation was often supported although infrequently examined (75.0 ± 15.3% of $n = 8$ species tested), whereas competition was supported in 53.8 ± 9.8% of species examined ($n = 26$) and host or food availability was supported in 50.0 ± 17.7% ($n = 8$ species). Interestingly, parasitism (including disease) was only examined in one species in our sample, and was not supported.

These general patterns were robust to subdividing the data in various ways. Similar patterns were found for elevational and latitudinal limits and for studies of 1–10 versus > 10 species (Fig. 2), although the proportion of species for which precipitation was examined and supported was greater for elevational limits than for latitudinal ones. Studies of animals

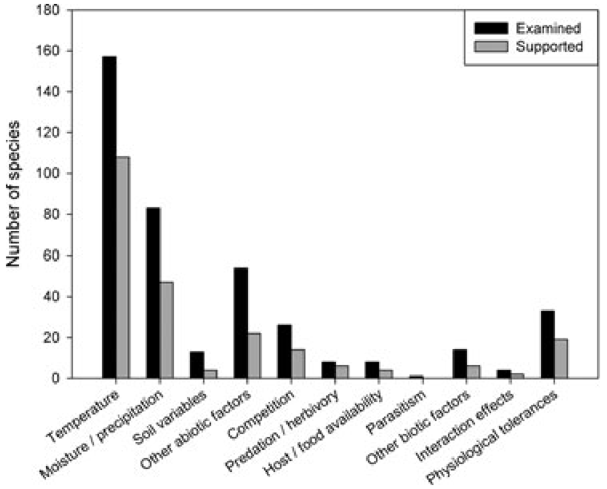

Figure 1 Number of species (out of 178) for which various abiotic and biotic factors were examined (black bars) and supported (grey bars) as setting their warm-edge range limits, from a global set of studies examining ≤ 10 species. Note that a single species may have been examined for (and may support) more than one factor.

and plants also showed similar patterns of factors examined and supported (Fig. 3), and both are dominated by studies that examined and supported temperature. However, precipitation (including soil moisture) was more frequently examined and supported in plants, and physiological tolerances were more frequently examined and supported in animals (Fig. 3a,b). Dividing terrestrial plant species into trees (n = 58 species) versus other growth forms (n = 36 species) showed that they have similar patterns to each other and to animals (Table 1). Temperature was the factor examined most often in both terrestrial and marine environments (Fig. 3c,d), but physiological tolerances were more frequently investigated in marine systems, in contrast to terrestrial systems (Fig. 3c,d). Although relatively few tropical species were included (n = 19), they show a similar pattern to the overall dataset (Table 2).

A key question in the study of warm-edge range limits is whether they are typically caused by biotic or abiotic factors (i.e. which is more common among species?). However, relatively few studies examined both (40 species, or 22.5% of all 178). Among these 40 species, many showed support for both categories of factors (n = 13), but support for abiotic factors only (n = 19) was more common than for biotic factors only (n = 7), with one study supporting neither type of factor. Thus, abiotic factors were supported significantly more often (G = 11.508, P < 0.001) among the 26 species that supported either abiotic or biotic factors. Only four species were explicitly tested for interaction effects between abiotic and biotic factors, and these were supported for two species.

In order to directly evaluate the relative importance of temperature and competition, we narrowed our analysis to studies that examined both (20 species; Table 3). Among

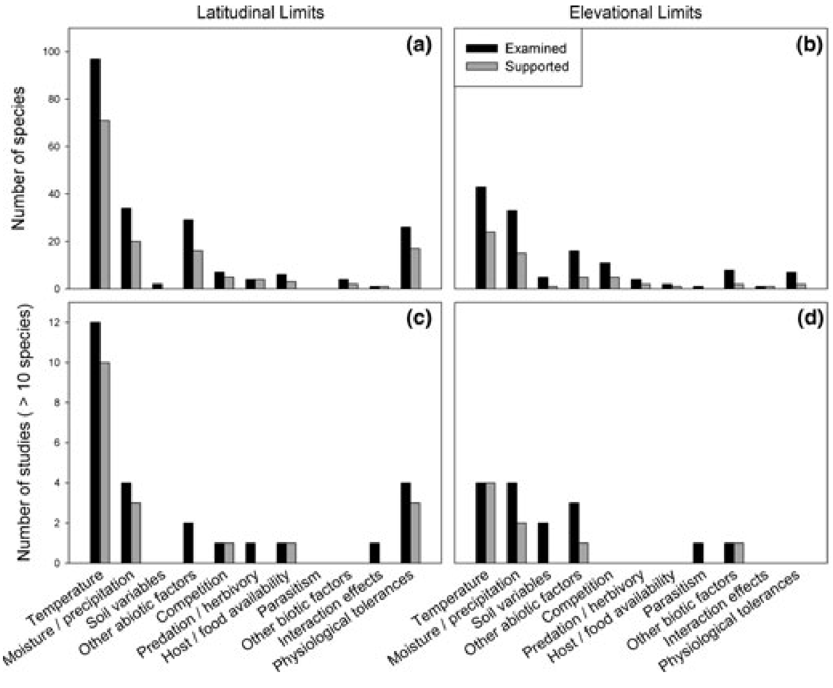

Figure 2 Factors that set species' warm-edge range limits, shown based on (a,b) the number of species and (c,d) the number of studies examining (black bars) and supporting (grey bars) various abiotic and biotic factors. Results are shown for: (a) latitudinal limits of single species in studies with ≤ 10 species, (b) elevational limits of single species in studies with ≤ 10 species, (c) latitudinal limits of species in studies with > 10 species, (d) elevational limits of species in studies with > 10 species. Note that a single study may examine (and support) more than one factor. Studies that examined > 10 species were counted such that any factor examined and supported in one or more species applied to the study as a whole.

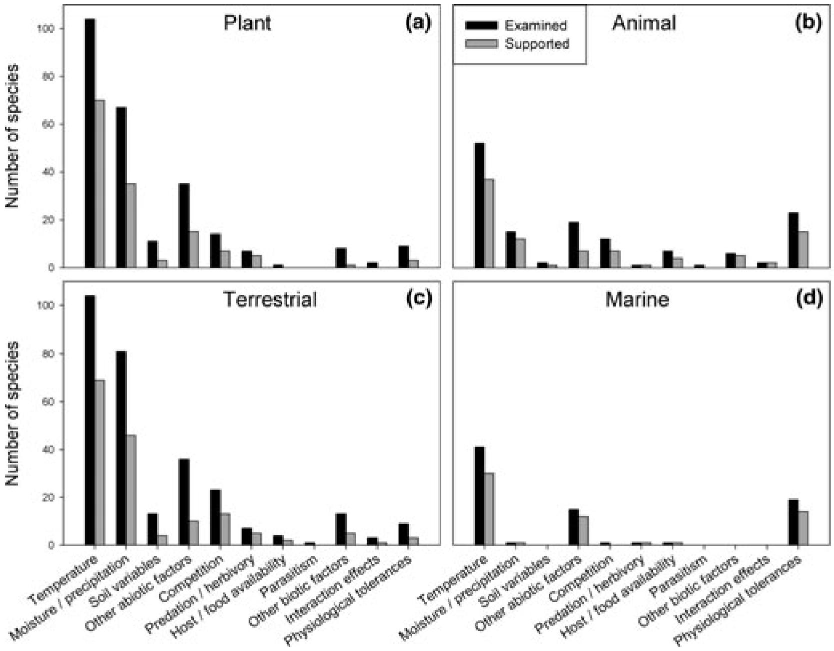

Figure 3 Number of species for which various abiotic and biotic factors were examined (black bars) and supported (grey bars) as setting their warm-edge range limits (from a pool of 178 species from studies that examined ≤ 10 species each), separated by: (a) plants (including algae), (b) animals, (c) terrestrial species, and (d) marine species.

Table 1 Factors that set species' warm-edge range limits in terrestrial plants, based on a synthesis from the literature, showing that factors are similar in trees (58 species) to those reported for other growth forms (36 species). Data are shown as the number of species that were examined for a given type of factor and the number of species in which that factor was supported. The overall dataset of studies with 10 or fewer species was reduced to include only studies of terrestrial plants.

	Trees (number of species)		Other growth forms (number of species)	
Factor	Examined	Supported	Examined	Supported
Temperature	55	39	31	20
Precipitation	47	26	20	9
Other soil	6	1	5	1
Other abiotic	20	3	12	11
Competition	10	5	3	1
Predation/herbivory	2	1	4	3
Host/food availability	1	0	0	0
Parasitism/disease	0	0	0	0
Other biotic	5	1	3	0
Abiotic–biotic interaction	2	0	0	0
Physiological tolerances	4	0	3	1

these species, four supported both temperature and competition, 11 supported temperature only, and four supported competition only, mirroring the results for all abiotic and biotic factors ($G = 6.794$, $P = 0.009$, $n = 15$).

Table 2 Factors that set warm-edge range limits in tropical species ($n = 19$), based on a synthesis from the literature. Species were taken from a set of studies that examined 10 species or fewer. Species were only included if they occurred unambiguously within the tropics or had their warm-edge range limit in the tropics.

	Number of species	
Factor	Examined	Supported
Temperature	19	16
Precipitation	10	5
Other soil	4	0
Other abiotic	6	4
Competition	5	3
Predation/herbivory	0	0
Host/food availability	1	0
Parasitism/disease	1	0
Other biotic	0	0
Abiotic–biotic interaction	2	0
Physiological tolerances	1	1

Proximate causes (a specific, mechanistic factor underlying the range limit of a species) for warm-edge range limits were determined for only 29 species in the database, plus two studies of > 10 species (Table 4, Fig. 4). We describe results for the 29 single species below. Many studies used laboratory or field experiments on physiological tolerances to explain the range limits of the target species ($n = 24$ species), often supplemented with further field observations or experiments ($n = 11$ species); only four species were studied with modelling. Most ($n = 22$ species) supported physiological

Table 3 The number of species for which competition or temperature (or both) were supported as potential factors explaining their warm-edge range limits, among a total of 20 species that were tested for both factors (from the full pool of 105 studies of ≤ 10 species; Appendix S1). The 'Proximate cause identified' column is a subset of the 20 total species. Based on a synthesis from the literature.

	Number of species				
Factor supported	All	Elevational	Latitudinal	Both	Proximate cause identified
Competition only	4	2	2	0	1
Temperature only	11	4	1	6	2
Both factors	4	2	1	1	1
Neither supported	1	1	0	0	0

Table 4 Hypothesized proximate causes of species' warm-edge range limits, based on a synthesis from the literature. Some studies tested multiple factors, but only some causes that are supported are listed. In studies of ≤ 10 species, all species supported the same proximate cause and have been combined to a single entry in this table; the full dataset is available in Appendix S1. Studies are grouped according to proximate cause. See Fig. 4 for results summarized by species and by factors supported versus examined.

Hypothesized proximate cause of range limit	Species	Taxon	Latitudinal or elevational limit?	Source
Abiotic factors				
Other abiotic factor: photoperiod limits reproduction	*Oxyria digyna*	Plant	Latitudinal	Heide (2005)
Other abiotic factor: occurrence of spring snow pack (necessary for successful reproduction)	*Gulo gulo*	Wolverine	Latitudinal, elevational	Copeland *et al.* (2010)
Physiological tolerance (water stress)	*Pinus* spp.	Tree (3 species)	Elevational	Barton (1993)
Physiological tolerances (temperature and precipitation)	*Plethodon jordani*	Salamander	Elevational	Gifford & Kozak (2012)
Physiological tolerances (temperature and precipitation)	*Silene ciliata*	Plant	Elevational	Giménez-Benavides *et al.* (2007, 2008)
Physiological tolerance (temperature)	Multiple	Algae (15 species)	Latitudinal	Bischoff-Basmann & Wiencke (1996)
Physiological tolerance (temperature)	*Mytilus edulis*	Mussel	Latitudinal	Jones *et al.* (2009, 2010)
Physiological tolerance (temperature)	*Giraudia sphacelarioides*	Alga	Latitudinal	Kristiansen & Pedersen (2005)
Physiological tolerance (temperature)	*Phyllophora pseudoceranoides*	Alga	Latitudinal	Molenaar & Breeman (1994)
Physiological tolerance (temperature)	*Iberolacerta cyreni*	Lizard	Elevational	Monasterio *et al.* (2010, 2011)
Physiological tolerance (temperature)	Multiple	Temperate trees (17 species)	Latitudinal	Morin *et al.* (2007)
Physiological tolerance (temperature)	Multiple	Algae (2 species)	Latitudinal	Orfanidis (1991)
Physiological tolerance (temperature)	Multiple	Algae (5 species)	Latitudinal	Orfanidis (1993)
Physiological tolerance (temperature)	*Scytosiphon lomentaria*	Alga	Latitudinal	Orfanidis *et al.* (1996)
Physiological tolerance (temperature)	*Eupogodon planus*	Alga	Latitudinal	Orfanidis *et al.* (1999)
Physiological tolerance (temperature)	*Zoarces viviparus*	Fish	Latitudinal	van Dijk *et al.* (1999); Pörtner *et al.* (2001)
Physiological tolerance (temperature)	*Semibalanus balanoides*	Barnacle	Latitudinal	Wethey & Woodin (2008)
Interacting factors				
Temperature-mediated competition	*Plethodon glutinosus*	Salamander	Latitudinal	Cunningham *et al.* (2009)
Biotic factors				
Competition	*Mnium arizonicum*	Moss	Elevational	Cleavitt (2004)
Competition	*Phylloscopus humei*	Bird	Latitudinal	Gross & Price (2000)
Herbivory	*Fucus radicans*	Alga	Latitudinal	Forslund *et al.* (2012)
Herbivory	*Polemonium viscosum*	Plant	Elevational	Galen (1990)
Predation	*Lepus americanus*	Snowshoe hare	Latitudinal	Sievert & Keith (1985)

tolerances to abiotic factors, especially tolerances related to temperature ($n = 16$), temperature and precipitation ($n = 2$), and precipitation/moisture only ($n = 3$). Support for biotic factors was found in five species, particularly predation or herbivory ($n = 3$) and competition ($n = 2$). The two studies of > 10 species, one on trees ($n = 17$ species) and one on algae ($n = 15$ species), also supported physiological tolerances to temperature.

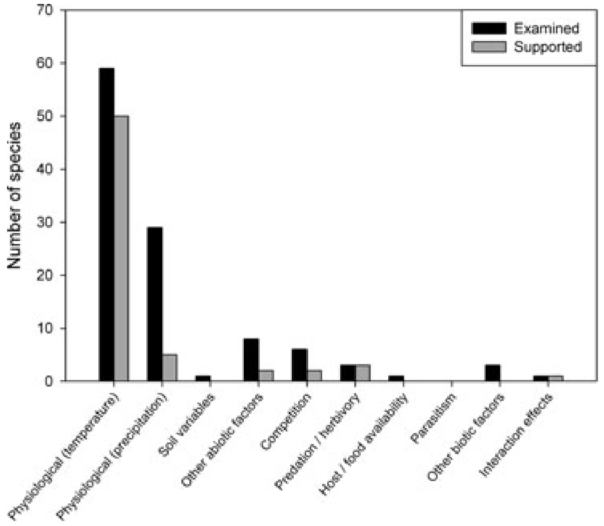

Figure 4 Number of species for which various abiotic and biotic factors were examined (black bars) and supported (grey bars) as proximate causes of their warm-edge range limits (61 total species). Note that a species may be examined for more than one factor.

Overall, patterns for these 29 (or 61) proximate-cause species were generally similar to those from the broader pool of 178 species. However, there is a potential for sampling biases given the smaller pool of species. For example, among the 29 species, 23 were sessile and only six were vertebrates. Sampling included both plants and animals, but with many algal species (12 of 29 species). Despite the potential for bias, patterns for vertebrates were broadly similar to those for other organisms, with physiological tolerances to abiotic factors frequently supported (19 of 23 for non-vertebrate species versus 3 of 6 for vertebrates only).

Among the 29 species, eight were tested for both biotic and abiotic proximate causes. Of these eight, five showed support for abiotic factors, two for biotic factors, and one species showed support for an interaction between abiotic and biotic factors. Only four were examined for both temperature and competition. Two species showed support for temperature (Monasterio *et al.*, 2010, 2011; Gifford & Kozak, 2012). A single species supported competition (Cleavitt, 2004). The fourth species (Cunningham *et al.*, 2009) supported temperature-mediated competition as the range-limiting factor.

DISCUSSION

Understanding the causes of warm-edge range limits is a critical question for many fields, but the general causes of these limits are unclear. Based on our systematic review, we found that many studies have addressed these causes, and many different abiotic and biotic factors are supported (Fig. 1). Contrary to the widespread assumption that biotic factors generally determine warm-edge limits (often attributed to MacArthur, 1972), most studies examined and also supported abiotic factors (especially temperature), both when considering all 178 species (Fig. 1) and when considering the set of 23 studies (61 species) for which proximate factors were identified. Among the studies in our overall database for which both biotic and abiotic factors were examined (40 species), significantly more species showed support for only abiotic factors ($n = 19$ species) than only biotic factors ($n = 7$ species). We found a similar pattern in studies that examined both temperature and competition, with four species supporting competition and 11 supporting temperature. We conclude that, based on our sample of published studies, there is little basis for assuming a greater importance of biotic factors than abiotic factors in setting warm-edge range limits, or a greater importance of competition than temperature.

However, many studies that tested both abiotic and biotic factors also found support for both types of factor (i.e. 13 of 40 species). Studies supporting both abiotic and biotic factors may reflect range limits set by biotic factors that change along an abiotic gradient (e.g. change in competition with temperature; Taniguchi & Nakano, 2000; Cunningham *et al.*, 2009), but it is unclear in most of these cases which factor (abiotic or biotic, or their interaction) is the actual proximate cause. Unfortunately, most studies did not explicitly test for interactions between abiotic and biotic factors (although such interactions might still be present regardless). Importantly, even if these interactions are widespread, our results do not support the idea that warm-edge range limits are typically set by biotic factors alone. Furthermore, cases that found no support for biotic factors seem unlikely to be supported by a combination of biotic and abiotic factors (i.e. if there is no support for competition, then it is unlikely that temperature + competition is the explanation).

After temperature, precipitation was by far the most frequently supported factor (47 of 178 species; Fig. 1). Interestingly, for elevational studies precipitation was supported nearly as often as temperature (Fig. 2), whereas for latitudinal studies precipitation was both tested and supported less frequently. Some species appear to have a 'dry edge' to their range: a range edge that is not the low-elevation or low latitude edge, but is seemingly set by changes in precipitation instead (e.g. *Clarkia xantiana xantiana*, an annual plant whose eastern range edge corresponds to a decline in precipitation due to a montane rain shadow; Geber & Eckhart, 2005; Eckhart *et al.*, 2010, 2011). We did not include these dry edges in our analysis, but they may impact the distributions of many species and may be important under anthropogenic climate change (given projected changes in rainfall patterns; IPCC, 2007). For example, ranges may shift in the opposite direction predicted by temperature changes due to changing precipitation patterns (e.g. downward shifts in elevation; Lenoir *et al.*, 2010; Crimmins *et al.*, 2011).

Proximate causes

We found that relatively few studies have tested the proximate causes of warm-edge range limits. Although many studies have shown relationships between warm-edge limits and climatic variables, the proximate causes remain unknown. Thus, rather than simply demonstrating that range limits are statistically related to temperature-based climatic variable(s), we need to determine how temperature limits species ranges. Many studies (approximately 80%; Appendix S1) used experiments to test proximate causes (e.g. transplant experiments, Sievert & Keith, 1985; Gaston, 2009; comparing performance of marginal and central populations, Cunningham *et al.*, 2009; Jones *et al.*, 2010). In some cases, statistical associations with temperature do seem to reflect physiological tolerances, but this should be tested explicitly. An alternative explanation is that other factors, both biotic and abiotic, covary with temperature, and that these other factors are the proximate causes.

In some cases, proximate causes may not matter. For example, species distribution models can often successfully predict species ranges (and related large-scale patterns) with climatic data alone (e.g. Pearson & Dawson, 2003; Araújo *et al.*, 2005; but see Hampe, 2004; Wisz *et al.*, 2013). However, there are circumstances where proximate causes are clearly important. For example, if warm-edge range limits shift in response to climate change, then the proximate factors that set these limits may be the factors that must be ameliorated to save populations and species from extinction (but see below). Proximate causes are also important for understanding the evolutionary basis of species range limits, given the potential for species to continually adapt and expand their ranges (Bridle & Vines, 2007; Kawecki, 2008). Finally, incorporating information on proximate causes should allow more accurate prediction of current ranges and range shifts (exemplified by recent studies of mechanistic distribution models; Buckley *et al.*, 2010b).

We find support for a diversity of proximate causes of warm-edge range limits (but especially physiological tolerances to temperature), including multiple categories of biotic interactions. One conspicuous exception is the absence of studies testing and supporting parasites and disease as factors setting warm-edge range limits. Given these results, the idea that these factors are common causes of species range limits (e.g. Ricklefs, 2010) clearly needs more study and cannot simply be assumed (at least not for warm edges). We also note that most species interactions examined were between two species, but multispecies interactions might also be important, especially in the tropics (Dobzhansky, 1950).

Potential biases

We acknowledge that our search was limited by the studies available in the published literature and that there are several potential sources of bias in our results (see also Materials and Methods). First, there is a tendency for studies to support factors that were tested. This may reflect the ability of researchers to accurately predict what factors are most likely to be important in their study system. On the other hand, alternative factors that are not explicitly tested cannot be ruled out as possible causes. Second, abiotic factors were tested more frequently than biotic ones. However, our main conclusions about the relative frequency of these factors among species are based on a set of species tested for both factors, and so should be robust to this source of bias. Third, our sample of 61 species with identified proximate causes is dominated by sessile organisms, and different factors may be important for vagile species relative to sessile ones. However, we found similar patterns in proximate causes of vertebrates relative to the dataset overall (i.e. limited physiological tolerances to abiotic factors often set range limits). Fourth, different factors might appear to be important at different spatial scales. However, by definition, proximate causes must operate at the local scale but apply to large-scale range limits. Nevertheless, scale may be an issue for other studies in our dataset. Fifth, the species studied occur predominantly in North America and Europe. The patterns found may be biased towards those in temperate regions (but note that latitudinal patterns for species entirely confined to the tropics might be difficult to interpret in terms of 'warm edges' per se). Further, results for our limited set of 19 tropical species are similar to those for the overall dataset (Table 2). Sixth, we were unable to perform a meta-analysis with our data, so our conclusions are based primarily on counts of species in which various factors are supported (although our question is how common these factors are across species, which our approach is best suited to answer). Similar vote counting approaches have been criticized (e.g. Harrison, 2011; Koricheva & Gurevitch, 2013), but the major criticism of these approaches (low statistical power) clearly does not apply to our statistically significant results. Finally, and perhaps most importantly, our conclusions depend on the original studies of warm-edge range limits that we summarize here. Determining the factors that set range limits is potentially very difficult, with many complicating factors. Many approaches have been used to reveal these factors (e.g. modelling, field observations, laboratory experiments), and the most effective studies may be those that combine diverse methods. Use of a single method may create biases (e.g. species distribution modelling favouring climatic factors). Testing these factors may also be complicated by the biology of the focal organism, including varying reproductive strategies among species, varying demographies or population trends within species (e.g. Morris *et al.*, 2008), and the potential for different factors to influence different life history stages of a single species (e.g. the vulnerable larval stage of many marine species; Pechenik, 1999). Different factors may also be important at different parts of the warm edge, or even at different times. Yet our results are largely consistent across both animals and plants (and further divisions within plants; Table 1), and so seem robust to much variation in general biology.

Comparison to other range-limit studies

Despite these potential biases, many of the patterns we found parallel those of other review papers on range limits. For example, Sexton *et al.* (2009) also found that many studies tested and supported abiotic factors (112 of 146), that a smaller number tested and supported biotic factors (31 of 51), and that many different biotic factors are supported as setting warm and cold range limits, but they did not specifically look at warm-edge limits. An important question for future studies is whether the factors that set cold-edge limits tend to differ from those setting warm-edge limits.

Our conclusions are based on summarizing the results of individual case studies, but other synthetic approaches to this topic are possible. As one example, Sunday *et al.* (2012) analysed a dataset of 142 marine and terrestrial ectotherm species to test if species' physiological limits correspond to climatic conditions at range limits. They found that warm-edge range limits in marine species generally correspond to physiological tolerances to temperature, whereas in terrestrial species they do not. They concluded that one explanation for this pattern is that warm-edge limits are set more often by biotic factors in terrestrial systems, in contrast to our results.

Comparison to studies of climate change impacts

Finally, a major motivation for our study was the potential for factors that set warm-edge range limits to become proximate causes of local extinction as ranges shift upwards and polewards due to anthropogenic climate change. Very few studies have directly examined the proximate causes of declines and extinction related to climate change (reviewed in Cahill *et al.*, 2013). Of those that did, the majority implicated interspecific interactions, in contrast to our results. One potential explanation for this difference is the limited taxonomic overlap between studies. The examples in Cahill *et al.* (2013) are dominated by non-sessile animals, particularly vertebrates, whereas those here are dominated by plants and sessile invertebrates. The importance of biotic interactions in causing local extinctions in vertebrates may also reflect abiotic impacts on organisms that serve as food or habitat. Ectotherms may be generally more sensitive to changing abiotic factors than endotherms (e.g. Aragón *et al.*, 2010). Also, the studies reviewed by Cahill *et al.* (2013) were not restricted to warm edges of species ranges, and factors causing local extinctions within a species' range might be different from those at the range limit. Finally, our initial assumption (that factors setting warm-edge range limits are generally the same factors causing extinction in these populations as a result of climate change) may be incorrect. A more thorough investigation of this assumption should be an urgent topic for future research.

CONCLUSIONS

Understanding the causes of warm-edge range limits is important both for understanding biogeographical patterns and (potentially) the impacts of global warming. It has often been assumed that warm-edge limits are set by biotic factors (e.g. competition) rather than abiotic factors (e.g. temperature). Surprisingly, our review spanning 178 species suggests that in the majority of species (108) warm-edge range limits are set at least partly by temperature. Furthermore, for those studies that tested both abiotic factors and biotic factors, biotic factors are supported less often than abiotic factors, and competition is supported less often than temperature. However, merely supporting temperature is not enough: it is critical to understand the proximate causes of range limits. Considering proximate causes reduces our pool to 61 species. Interestingly, for most species, physiological tolerances to temperature are supported as the proximate cause rather than biotic factors, although very few studies tested both types of factors. The limited number of studies identifying proximate causes represents an important gap in our understanding of range limits.

We make two recommendations for future empirical studies. First, in order to determine what sets warm-edge limits, it is necessary to identify proximate causes, not just test associations between geographical limits and climatic variables. Second, it is important to test multiple factors. For instance, to directly assess the relative roles of temperature and competition in determining warm-edge limits, more studies are needed that examine both factors and their interactions.

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REFERENCES

Alexander, J.M. & Edwards, P.J. (2010) Limits to the niche and range margins of alien species. *Oikos*, **119**, 1377–1386.

Anderson, B.J., Akçakaya, H.R., Araújo, M.B., Fordham, D.A., Martinez-Meyer, E., Thuiller, W. & Brook, B.W. (2009) Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1415–1420.

Angilletta, M.J. (2009) *Thermal adaptation: a theoretical and empirical synthesis*. Oxford University Press, Oxford.

Aragón, P., Rodríguez, M.A., Olalla-Tárraga, M.A. & Lobo, J.M. (2010) Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms. *Animal Conservation*, **13**, 363–373.

Araújo, M.B., Pearson, R.G., Thuiller, W. & Erhard, M. (2005) Validation of species–climate impact models under climate change. *Global Change Biology*, **11**, 1504–1513.

Barton, A. (1993) Factors controlling plant-distributions – drought, competition, and fire in montane pines in Arizona. *Ecological Monographs*, **63**, 367–397.

Bischoff-Basmann, B. & Wiencke, C. (1996) Temperature requirements for growth and survival of Antarctic Rhodophyta. *Journal of Phycology*, **32**, 525–535.

Bridle, J.R. & Vines, T.H. (2007) Limits to evolution at range margins: when and why does adaptation fail? *Trends in Ecology and Evolution*, **22**, 140–147.

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A.T. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. *Ecology Letters*, **10**, 701–709.

Brown, J.H., Stevens, G.C. & Kaufman, D.M. (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.

Buckley, L.B., Davies, T.J., Ackerly, D.D., Kraft, N.J.B., Harrison, S.P., Anacker, B.L., Cornell, H.V., Damschen, E.I., Grytnes, J.A., Hawkins, B.A., McCain, C.M., Stephens, P.R. & Wiens, J.J. (2010a) Phylogeny, niche conservatism and the latitudinal diversity gradient in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2131–2138.

Buckley, L.B., Urban, M.C., Angilletta, M.J., Crozier, L.G., Rissler, L.J. & Sears, M.W. (2010b) Can mechanism inform species' distribution models? *Ecology Letters*, **13**, 1041–1054.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O. & Wiens, J.J. (2013) How does climate change cause extinction? *Proceedings of the Royal Society B: Biological Sciences*, **280**, 20121890.

Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Cleavitt, N. (2004) Comparative ecology of a lowland and a subalpine species of *Mnium* in the northern Rocky Mountains. *Plant Ecology*, **174**, 205–216.

Copeland, J.P., McKelvey, K.S., Aubry, K.B., Landa, A., Persson, J., Inman, R.M., Krebs, J., Lofroth, E., Golden, H., Squires, J.R., Magoun, A., Schwartz, M.K., Wilmot, J., Copeland, C.L., Yates, R.E., Kojola, I. & May, R. (2010) The bioclimatic envelope of the wolverine (*Gulo gulo*): do climatic constraints limit its geographic distribution? *Canadian Journal of Zoology*, **88**, 233–246.

Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T. & Mynsberge, A.R. (2011) Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**, 324–327.

Cunningham, H.R., Rissler, L.G. & Apodaca, J.J. (2009) Competition at the range boundary in the slimy salamander: using reciprocal transplants for studies on the role of biotic interactions in spatial distributions. *Journal of Animal Ecology*, **78**, 52–62.

van Dijk, P.L.M., Tesch, C., Hardewig, I. & Pörtner, H.O. (1999) Physiological disturbances at critically high temperatures: a comparison between stenothermal Antarctic and eurythermal temperate eelpouts (Zoarcidae). *Journal of Experimental Biology*, **202**, 3611–3621.

Dobzhansky, T. (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.

Eckhart, V.M., Singh, I., Louthan, A.M., Keledjian, A.J., Chu, A., Moeller, D.M. & Geber, M.A. (2010) Plant–soil water relations and the species border of *Clarkia xantiana* ssp. *xantiana* (Onagraceae). *International Journal of Plant Sciences*, **171**, 749–760.

Eckhart, V.M., Geber, M.A., Morris, W.F., Fabio, E.S., Tiffin, P. & Moeller, D.M. (2011) The geography of demography: long-term demographic studies and species distribution models reveal a species border limited by adaptation. *The American Naturalist*, **178**, S26–S43.

Forslund, H., Eriksson, O. & Kautsky, L. (2012) Grazing and geographic range of the Baltic seaweed *Fucus radicans* (Phaeophyceae). *Marine Biology Research*, **8**, 322–330.

Galen, C. (1990) Limits to the distributions of alpine tundra plants – herbivores and the alpine skypilot, *Polemonium viscosum*. *Oikos*, **59**, 355–358.

Gaston, K.J. (2003) *The structure and dynamics of geographic ranges*. Oxford University Press, Oxford.

Gaston, K.J. (2009) Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 1395–1406.

Geber, M.A. & Eckhart, V.M. (2005) Experimental studies of adaptation in *Clarkia xantiana* (Onagraceae). II. Fitness variation across a subspecies border. *Evolution*, **59**, 521–531.

Gelman, A. & Hill, J. (2007) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge.

Giehl, E.L.H. & Jarenkow, J.A. (2012) Niche conservatism and the differences in species richness at the transition of tropical and subtropical climates in South America. *Ecography*, **35**, 933–943.

Gifford, M.E. & Kozak, K.H. (2012) Islands in the sky or squeezed at the top? Ecological causes of elevational range limits in montane salamanders. *Ecography*, **35**, 193–203.

Giménez-Benavides, L., Escudero, A. & Iriondo, J.M. (2007) Local adaptation enhances seedling recruitment along an altitudinal gradient in a high mountain Mediterranean plant. *Annals of Botany*, **99**, 723–734.

Giménez-Benavides, L., Escudero, A. & Iriondo, J.M. (2008) What shapes the altitudinal range of a high mountain Mediterranean plant? Recruitment probabilities from ovule to seedling stage. *Ecography*, **31**, 731–740.

Gross, S.J. & Price, T.D. (2000) Determinants of the northern and southern range limits of a warbler. *Journal of Biogeography*, **27**, 869–878.

Gurevitch, J. & Hedges, L.V. (2001) Meta-analysis: combining the results of independent experiments. *Design and analysis of ecological experiments* (ed. by S.M. Scheiner and J. Gurevitch), pp. 347–369. Oxford University Press, Oxford.

Hampe, A. (2004) Bioclimatic envelope models: what they detect and what they hide. *Global Ecology and Biogeography*, **13**, 469–471.

Hampe, A. & Jump, A.S. (2011) Climate relicts: past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 313–333.

Harrison, F. (2011) Getting started with meta-analysis. *Methods in Ecology and Evolution*, **2**, 1–10.

Heide, O.M. (2005) Ecotypic variation among European arctic and alpine populations of *Oxyria digyna*. *Arctic, Antarctic and Alpine Research*, **37**, 233–238.

Heller, H.C. (1971) Altitudinal zonation of chipmunks (*Eutamias*) – interspecific agression. *Ecology*, **52**, 312–319.

Hickling, R., Roy, D.B., Hill, J.K. & Thomas, C.D. (2005) A northward shift of range margins in the British Odonata. *Global Change Biology*, **11**, 502–506.

Hillebrand, H. (2004) On the generality of the latitudinal biodiversity gradient. *The American Naturalist*, **163**, 192–211.

IPCC (2007) *Climate change 2007: synthesis report. Contributions of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by the Core Writing Team, R.K. Pachauri and A. Reisinger). Intergovernmental Panel on Climate Change, Geneva.

Janzen, D.H. (1981) The peak in North American ichneumonid species richness lies between 38° and 42° N. *Ecology*, **62**, 532–537.

Jones, S.J., Mieszkowska, N. & Wethey, D.S. (2009) Linking thermal tolerances and biogeography: *Mytilus edulis* (L.) at its southern limit on the east coast of the United States. *Biological Bulletin*, **217**, 73–85.

Jones, S.J., Lima, F.P. & Wethey, D.S. (2010) Rising environmental temperatures and biogeography: poleward range contraction of the blue mussel, *Mytilus edulis* L., in the western Atlantic. *Journal of Biogeography*, **37**, 2243–2259.

Jones, S.J., Southward, A.J. & Wethey, D.S. (2012) Climate change and historical biogeography of the barnacle *Semibalanus balanoides*. *Global Ecology and Biogeography*, **21**, 716–724.

Kaufman, D.M. (1995) Diversity of New World mammals: universality of the latitudinal gradients of species and bauplans. *Journal of Mammalogy*, **76**, 322–334.

Kawecki, T.J. (2008) Adaptation to marginal habitats. *Annual Review of Ecology, Evolution, and Systematics*, **39**, 321–342.

Koricheva, J. & Gurevitch, J. (2013) Place of meta-analysis among other methods of research synthesis. *Handbook of meta-analysis in ecology and evolution* (ed. by J. Koricheva, J. Gurevitch and K. Mengersen) pp. 3–13. Princeton University Press, Princeton, NJ.

Kozak, K.H. & Wiens, J.J. (2006) Does niche conservatism drive speciation? A case study in North American salamanders. *Evolution*, **60**, 2604–2621.

Kozak, K.H. & Wiens, J.J. (2010) Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American Naturalist*, **176**, 40–54.

Kristiansen, A. & Pedersen, P.M. (2005) *Giraudia sphacelarioides* (Phaeophyceae) at the Canary Islands and in Danish waters: a study in ecotypic differentiation and its biogeographical implications. *Nordic Journal of Botany*, **23**, 735–742.

Lenoir, J., Gégout, J.-C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W. & Svenning, J.-C. (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**, 295–303.

Li, J., He, Q., Hua, X., Zho, J., Xu, H., Chen, J. & Fu, C. (2009) Climate and history explain the species richness peak at mid-elevation for *Schizothorax* fishes (Cypriniformes, Cyprinidae) distributed in the Tibetan Plateau and its adjacent regions. *Global Ecology and Biogeography*, **18**, 264–272.

Lowry, E., Rollinson, E.J., Laybourn, A.J., Scott, T.E., Aiello-Lammens, M.E., Gray, S.M., Mickley, J. & Gurevitch, J. (2012) Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution*, **3**, 182–196.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.

McCain, C.M. (2005) Elevational gradients in diversity of small mammals. *Ecology*, **86**, 366–372.

McCain, C.M. (2007) Area and mammalian elevational diversity. *Ecology*, **88**, 76–86.

McCain, C.M. (2009) Global analysis of bird elevational diversity. *Global Ecology and Biogeography*, **18**, 346–360.

Molenaar, F.J. & Breeman, A.M. (1994) Ecotypic variation in *Phyllophora pseudoceranoides* (Rhodophyta) ensures winter reproduction throughout its geographic range. *Journal of Phycology*, **30**, 392–402.

Monasterio, C., Salvador, A. & Díaz, J.A. (2010) Altitude and rock cover explain the distribution and abundance of a Mediterranean alpine lizard. *Journal of Herpetology*, **44**, 158–163.

Monasterio, C., Shoo, L.P., Salvador, A., Siliceo, I. & Díaz, J.A. (2011) Thermal constraints on embryonic development as a proximate cause for elevational range limits in two Mediterranean lacertid lizards. *Ecography*, **34**, 1030–1039.

Morin, X., Augspurger, C. & Chuine, I. (2007) Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology*, **88**, 2280–2291.

Morris, W.F., Pfister, C.A., Tuliapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S., Bruno, E.M., Church, D.R., Coulson, T., Doak, D.F., Forsyth, S., Gaillard, J.-M., Horvitz, C.C., Kalisz, S., Kendall, B.E., Knight, T.M., Lee, C.T. & Menges, E.S. (2008) Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, **89**, 19–25.

Orfanidis, S. (1991) Temperature responses and distribution of macroalgae belonging to the warm-temperate Mediterranean–Atlantic distribution group. *Botanica Marina*, **34**, 541–552.

Orfanidis, S. (1993) Temperature responses and distribution of several Mediterranean macroalgae belonging to different distribution groups. *Botanica Marina*, **36**, 359–370.

Orfanidis, S., Haritonidis, S. & Tsekos, I. (1996) Temperature requirements of *Scytosiphon lomentaria* (Scytosiphonales, Phaeophyta) from the Gulf of Thessaloniki, Greece, in relation to geographic distribution. *Helgolander Meeresuntersuchungen*, **50**, 15–24.

Orfanidis, S., Venekamp, L. & Breeman, A. (1999) Ecophysiological adaptations of two Mediterranean red algae in relation to distribution. *European Journal of Phycology*, **34**, 469–476.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, **37**, 637–669.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Parmesan, C., Gaines, S., Gonzalez, L., Kaufman, D.M., Kingsolver, J., Peterson, A.T. & Sagarin, R. (2005) Empirical perspectives on species borders: from traditional biogeography to global change. *Oikos*, **108**, 58–75.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimatic envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Pechenik, J.A. (1999) On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Marine Ecology Progress Series*, **177**, 269–297.

Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005) Climate change and distribution shifts in marine species. *Science*, **308**, 1912–1915.

Peterson, A.T. (2003) Predicting the geography of species' invasions via ecological niche modeling. *Quarterly Review of Biology*, **78**, 419–433.

Peterson, A.T. & Nyári, Á.S. (2007) Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner *Shiffornis* sp., in the tropics. *Evolution*, **62**, 173–183.

Pörtner, H.O., Berdal, B., Blust, R., Brix, O., Colosimo, A., De Wachter, B., Guiliani, A., Johansen, T., Fischer, T., Knust, R., Lannig, G., Naevdal, G., Nedenes, A., Nyhammer, G., Sartoris, F.J., Serendero, I., Sirabella, P., Thorkildsen, S. & Zakhartzev, M. (2001) Climate induced temperature effects on growth performance, fecundity and recruitment in marine fish: developing a hypothesis for cause and effect relationships in Atlantic cod (*Gadus morhua*) and common eelpout (*Zoarces viviparus*). *Continental Shelf Research*, **21**, 1975–1997.

Pullin, A.S. & Stewart, G.B. (2006) Guidelines for systematic review in conservation and environmental management. *Conservation Biology*, **20**, 1647–1656.

R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org/.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200–205.

Rahbek, C. (1997) The relationship among area, elevation, and regional species richness in Neotropical birds. *The American Naturalist*, **149**, 875–902.

Ricklefs, R.E. (2010) Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences USA*, **107**, 1265–1272.

Rohlf, F.J. & Slice, D.E. (2008) *BIOMstat for Windows*. Exeter Software, Setauket, NY.

Savage, J. & Cavender-Bares, J. (2012) Habitat specialization and the role of trait lability in structuring diverse willow (Salicaceae) communities. *Ecology*, **93**, S138–S150.

Sexton, J.P., McIntyre, P.J., Angert, A.L. & Rice, K.J. (2009) Evolution and ecology of species range limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–436.

Sievert, P.R. & Keith, L.B. (1985) Survival of snowshoe hares at a geographic range boundary. *Journal of Wildlife Management*, **49**, 854–866.

Smith, S.A., Stephens, P.R. & Wiens, J.J. (2005) Replicate patterns of species richness, historical biogeography, and phylogeny in Holarctic treefrogs. *Evolution*, **59**, 2433–2450.

Smith, S.A., Nieto Montes de Oca, A., Reeder, T.W. & Wiens, J.J. (2007) A phylogenetic perspective on elevational species richness patterns in Middle American treefrogs: why so few species in lowland tropical rainforests? *Evolution*, **61**, 1188–1207.

Somero, G.N. (2012) The physiology of global change: linking patterns to mechanisms. *Annual Review of Marine Science*, **4**, 39–61.

Stephens, P.R. & Wiens, J.J. (2009) Bridging the gap between community ecology and historical biogeography: niche conservatism and community structure in emydid turtles. *Molecular Ecology*, **18**, 4664–4679.

Sunday, J.M., Bates, A.E. & Dulvy, N.K. (2012) Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, **2**, 686–690.

Taniguchi, Y. & Nakano, S. (2000) Condition-specific competition: implications for the altitudinal distribution of stream fishes. *Ecology*, **81**, 2027–2039.

Thomas, C.D. (2010) Climate, climate change, and range boundaries. *Diversity and Distributions*, **16**, 488–495.

Wethey, D.S. (2002) Biogeography, competition, and microclimate: the barnacle *Chthamalus fragilis* in New England. *Integrative and Comparative Biology*, **42**, 872–880.

Wethey, D.S. & Woodin, S.A. (2008) Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. *Hydrobiologia*, **606**, 139–151.

Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P. & Brannock, P.M. (2011) Response of intertidal populations to climate: effects of extreme events versus long term change. *Journal of Experimental Marine Biology and Ecology*, **400**, 132–144.

Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist*, **168**, 579–596.

Wiens, J.J., Parra-Olea, G., García-París, M. & Wake, D.B. (2007) Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society B: Biological Sciences*, **274**, 919–928.

Wisz, M.S., Pottier, J., Kissling, W.D. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modeling. *Biological Reviews*, **88**, 15–30.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Summary data from 125 studies of species' warm-edge range limits.

BIOSKETCH

This paper arose from a seminar on species' responses to climate change in the Department of Ecology and Evolution at Stony Brook University, New York. The authors have many diverse research interests.

Author contributions: A.E.C., M.E.A.-L. and J.J.W. wrote the manuscript. All authors contributed to revisions and performed literature reviews. J.J.W. conceived the study.

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