Review & synthesis

Climate-related range shifts – a global multidimensional synthesis and new research directions

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Poleward and upward shifts are the most frequent types of range shifts that have been reported in response to contemporary climate change. However, the number of reports documenting other types of range shifts – such as in east-west directions across longitudes or, even more unexpectedly, towards tropical latitudes and lower elevations – is increasing rapidly. Recent studies show that these range shifts may not be so unexpected once the local climate changes are accounted for. We here provide an updated synthesis of the fast-moving research on climate-related range shifts. By describing the current state of the art on geographical patterns of species range shifts under contemporary climate change for plants and animals across both terrestrial and marine ecosystems, we identified a number of research shortfalls. In addition to the recognised geographic shortfall in the tropics, we found taxonomic and methodological shortfalls with knowledge gaps regarding range shifts of prokaryotes, lowland range shifts of terrestrial plants, and bathymetric range shifts of marine plants. Based on this review, we provide a research agenda for filling these gaps. We outline a comprehensive framework for assessing multidimensional changes in species distributions, which should then be contrasted with expectations based on climate change indices, such as velocity measures accounting for complex local climate changes. Finally, we propose a unified classification of geographical patterns of species range shifts, arranged in a bi-dimensional space defined by species' persistence and movement rates. Placing the observed and expected shifts into this bi-dimensional space should lead to more informed assessments of extinction risks.

Latitude, longitude and elevation or depth – in marine ecosystems – constitute the geographic dimensions over which a species' range is estimated, and a species' range shift is defined as any changes in distribution along these geographic dimensions over the fourth dimension, time (Lenoir and Svenning 2013). Species range shifts are now increasingly a reality, with latitudinal and elevational range shifts being especially well documented for a wide variety of eukaryotic groups such as algae, lichens, mosses, vascular plants, molluscs, crustaceans, insects, fishes, amphibians, reptiles, birds and mammals (Barry et al. 1994, Thomas and Lennon 1999, van Herk et al. 2002, Perry et al. 2005, Whitfield et al. 2007, Lenoir et al. 2008, McMenamin et al. 2008, Moritz et al. 2008, Bergamini et al. 2009, Chen et al. 2009, Wernberg et al. 2011, Przeslawski et al. 2012), chiefly between 30°N and 60°N latitudes (Lenoir and Svenning 2013). These shifts are often strongly linked to recent global temperature increase (Parmesan and Yohe 2003, Chen et al. 2011, Gottfried et al. 2012, Poloczanska et al. 2013).

Increase in temperature is likely to have a directional impact on species range shifts, because temperatures are autocorrelated in space, linking warmer conditions at lower latitudes or elevations (shallower depths in the ocean) with cooler conditions at higher latitudes or elevations (deeper depths in the ocean). Therefore, one expects anisotropic and predominantly uni-directional poleward or upward (bottomward in the ocean) range shifts as climate warms. Accordingly, a new global meta-analysis has estimated the velocity of distribution changes (geographic shifts of species distributions over time) under contemporary climate change to have occurred with a median rate of 1.69 km yr^{-1} towards higher latitudes in the Northern Hemisphere and a median rate of 1.1 m yr^{-1} towards higher elevations in mountain ecosystems (Chen et al. 2011). The authors also found a strong correlation between these observed velocities of distribution changes and the observed velocities of temperature changes (geographic shifts of isotherms over time) (Loarie et al. 2009). However, recent studies have challenged this uni-dimensional (latitude or elevation/depth), uni-directional (poleward or upward/bottomward) and uni-variate (temperature) perspective on the fingerprint of anthropogenic climate change on species range shifts (Comte and Grenouillet 2013, Pinsky et al. 2013, VanDerWal et al. 2013) as it ignores the potentially complex mosaic of local climate changes involving interactions among temperature, precipitation, species-specific tolerances, competitive release and land-use changes (Lenoir et al. 2010).

Based on the observed velocities of both temperature and precipitation changes across Australia from 1950 to 2010, VanDerWal et al. (2013) computed the necessary velocities of distribution changes required by 464 bird species to track their climatic niches. The study estimated the required distribution shifts to be multidimensional, including not only poleward, but also equatorward, eastward and westward range shifts. Using a bi-dimensional approach for the geographical space (latitude and longitude) and the ecological niche (temperature and precipitation), the authors found much faster required velocities of distribution changes than expected on the basis of temperature alone and considering only latitudinal gradients. Such findings suggest that the focus on uni-dimensional and uni-directional shifts in species distributions driven by temperature alone is likely to underestimate the actual fingerprint of climate change (VanDerWal et al. 2013). From a warming perspective, unexpected range shifts in east-west directions across longitudes or, even more so, towards tropical latitudes and lower elevations, linked to complex interactions among temperature, precipitation and biotic factors, have already been reported (Jepsen et al. 2008, Lenoir et al. 2010, Crimmins et al. 2011, Keith et al. 2011, Mattila et al. 2011, Pinsky et al. 2013, Cannone and Pignatti 2014), as have stable ranges, i.e. lacking range shifts (Moritz et al. 2008, Bertrand et al. 2011). These complex range shifts support the idea that the climate changes realized during the 20th century may have driven a variety of range shifts deviating from the simple uni-dimensional and uni-directional range shift predictions (Burrows et al. 2011). Unfortunately, multidimensional assessments of species range shifts along all three geographic dimensions (latitude, longitude and elevation or depth) simultaneously are largely lacking (but see Engelhard et al. 2011, Comte and Grenouillet 2013).

In addition to these three geographic dimensions, species range shifts are usually described through changes occurring in specific distribution parameters, such as range margins, range core or abundance (Lenoir and Svenning 2013). The earliest detection of species range shifts under 20th century climate change have come from work at range margins, documenting colonization and establishment events at the leading edge (Parmesan et al. 1999, Walther et al. 2005, Hickling et al. 2006, Moritz et al. 2008, Alheit et al. 2012) or local extinction events at the trailing edge (Parmesan et al. 1999, Lesica and McCune 2004, Orensanz et al. 2004, Wilson et al. 2005, Franco et al. 2006, Moritz et al. 2008, Murphy et al. 2010, Zhu et al. 2012). More subtle changes inside species' ranges have also been detected, notably at the range core (Lenoir et al. 2008). Even more subtle changes within the ranges of species can be inferred by comparing historical and modern data on species abundance within a locality (Parmesan 2006). Because species have a tendency, albeit a noisy one, for being most abundant in the center of their range and decline gradually towards range margins (Sagarin et al. 2006), distribution changes in response to climate warming should be evident by shifts in abundance within a locality: species adapted to cooler conditions should decline, while warm-adapted species should increase (Barry et al. 1994). Based on this idea, several studies have already reported species range shifts from changes in abundance (Beaugrand et al. 2003, Atkinson et al. 2004, Møller et al. 2008, Jiguet et al. 2010, Virkkala and Rajasärkkä 2011, Dolanc et al. 2013). In

some cases, quantitative changes within species ranges can be considerable without any observable change in overall range extent (Virkkala and Rajasärkkä 2011). Although changes in species abundance within their range are not strictly classified as species range shifts per se, these can be considered as intermediate states in an ongoing shifting process or early signs of species range shifts (Maggini et al. 2011). For this reason, range-shift detection should not be restricted to colonization and extinction events at the leading edge and trailing edge, respectively, but also cover within-distribution changes by focusing on changes in the optimum position as well as abundance changes.

Based on these four descriptors of a distribution (leading edge, trailing edge, optimum, abundance), many different terms have been used in the literature to refer to the many ways species may shift their distribution as climate warms (Breshears et al. 2008, Maggini et al. 2011), amongst others: leading-edge expansion, trailing-edge retraction, optimum shift, and abundance changes. However, very few studies so far have provided a comprehensive picture of climate-related shifts in species distributions by focusing on all four distribution parameters simultaneously for a given species (Kelly and Goulden 2008, Maggini et al. 2011, Lehikoinen et al. 2013). In fact, we are aware of only a single study that did so throughout an entire species' range (Lehikoinen et al. 2013).

Using all three geographic dimensions (latitude, longitude and elevation or depth) as well as all four distribution parameters (leading edge, trailing edge, optimum, abundance) to describe the current state of the art on the observed patterns of species range shifts under contemporary climate change, this review aims to identify knowledge gaps in relation to geography (where), taxonomy (what) and methodology (how). Based on this review, we provide a working agenda for future challenges in this research area to suggest where (geographic regions), what (taxonomic groups) and how (methodological approaches) we should be looking next. Finally, to help assess species' extinction risks, we propose to categorize the full set of possible types of changes in species ranges in a unified classification arranged in a bi-dimensional space, defined by species' persistence rate (SPR) and species' movement rate (SMR).

Material and methods

We first performed an exhaustive literature survey to collect information on geographical patterns of species range shifts under contemporary climate change and then analysed the collected data to describe the current state of the art and discuss potential future challenges.

Literature survey

Using specific search queries (Supplementary material Appendix 1) and covering both terrestrial and marine ecosystems, we investigated the peer-reviewed literature on climate-related range shifts under contemporary climate change and found a total of 245 publications. By contemporary climate change, we here mean the period stretching from

the 1850s and onwards. For 212 out of 245 publications, we were able to extract information on whether or not the study reported changes in species' distributions by focusing on one or several of the following distribution parameters: latitude, longitude, elevation/depth, leading edge, trailing edge, optimum and abundance (Supplementary material Appendix 2). To identify current shortfalls in the literature regarding these seven studied distribution parameters and to suggest where (geographic regions), what (taxonomic groups) and how (methodological approaches) we should be looking next, we retrieved the following information for each study (Supplementary material Appendix 3): ecosystem (ECO: marine [M] vs terrestrial [T]); kingdom (TAX: animal [A] vs plant [P]); total number of taxa (N); starting year (START); ending year (END); time period (DUR); western longitudinal boundary (XMIN); eastern longitudinal boundary (XMAX); longitudinal extent (XEXT); southern latitudinal boundary (YMIN); northern latitudinal boundary (YMAX); latitudinal extent (YEXT); and total surface area (AREA). Note that all photosynthetic eukaryotic organisms were considered as plants here.

Data analyses

We ran a constrained correspondence analysis (CCA) on the matrix containing binary information (0/1) for the seven distribution parameters considered (Supplementary material Appendix 2, Table A2) with ECO and TAX as categorical explanatory variables and N, AREA, START and END as continuous explanatory variables. Such a constrained multivariate analysis is useful for displaying the variation explained by a set of explanatory variables. We used ECO and TAX as biological constraints because we expected differences between terrestrial and marine ecosystems as well as between plants and animals with respect to how climate-related range shifts are currently studied. Indeed, stemming from a lack of research effort along the latitudinal gradient, it has already been highlighted for woody plants that reports of latitudinal range retractions are sparse compared to reports of elevational range retractions, leading to the so called altitude-for-latitude disparity in range retractions of woody plants (Jump et al. 2009). Additionally, it has been demonstrated that both range edges have been equally responsive in marine ectotherms, whereas the trailing edge has been less responsive than the leading edge in terrestrial ectotherms (Sunday et al. 2012). This leading-edge-for-trailing-edge disparity in the range shifts of terrestrial ectotherms could either reflect real biological differences or stem from a lack of research effort at the trailing edge compare to the leading edge in terrestrial ecosystems. We used START and END as time constraints because we assumed that more studies used historical records from recent censuses (1970s onwards) than from earlier periods. Indeed, the oldest historical records are not only scarce and difficult to retrieve, but also particularly challenging to use for comparison with modern records because these historical records were usually collected using outdated methodologies, leading to a limited utility of such data (Tingley and Beissinger 2009). We used AREA as a spatial constraint because we expected that more studies focused on relatively small geographical areas to detect climate-related range shifts. Not only are old historical records scarce and difficult to retrieve, but historical records are also difficult to gather across large geographical areas, thus constraining our ability to study species range shifts at a global scale. Finally, we used N as a sampling-effort constraint. All multivariate analyses were carried out in R 3.0.0 (R Development Core Team) using the 'ade4' package.

Results

By using the 212 selected studies to describe the current state of the art regarding observed range shifts under contemporary climate change, we identified geographic, taxonomic and methodological research shortfalls.

Geographic shortfalls

We found 123 and 89 studies focusing on the terrestrial and marine ecosystems, respectively. Research on terrestrial and marine range shifts has in general been far more frequent in the Northern Hemisphere than in the Southern Hemisphere (Fig. 1 and 2), as already been mentioned elsewhere (Lenoir and Svenning 2013). However, this discrepancy was much less pronounced for marine (Fig. 2) than for terrestrial studies (Fig. 1). Hotspots of research efforts are currently located in Europe with hubs in the Alps, Fennoscandia, the British Isles and the North Sea.

On land, research efforts are weak in Asia, South America, central Africa, Greenland and Antarctica (Fig. 1a), where studies covering large geographic extents are truly lacking (but see Peh 2007, Feeley 2012). Notably, only a few local studies restricted to tiny ecoregions and thus difficult to spot on the global map (Fig. 1a) have reported climate-related range shifts in Antarctica (Smith 1994, Le Roux and McGeoch 2008), South America (Forero-Medina et al. 2011) and Asia (Tougou et al. 2009, Jump et al. 2012, Telwala et al. 2013). Evidence in Europe and North America is mainly from Mediterranean woodlands, temperate broadleaved and mixed forests, temperate conifer forests, boreal forests and tundra ecosystems (Fig. 1b). The number of reports from tropical and subtropical forests (Pounds et al. 1999, Raxworthy et al. 2008, Chen et al. 2009, Feeley et al. 2011), tropical and subtropical grasslands savannahs and shrublands (Hockey et al. 2011, Chirima et al. 2012, Sirami and Monadjem 2012) and deserts and xeric shrublands (Sinervo et al. 2010, Hockey et al. 2011) is relatively low, but has recently begun to increase. Except from the temperate biome, research efforts on species range shifts have focused chiefly on the coldest biomes (tundra, boreal and alpine), with much less research efforts in the hottest places on Earth such as the tropics (Fig. 1b), despite the fact that tropical biomes cover a large proportion of land area and harbour most of Earth's biodiversity, thus deserving particular attention.

Global coverage is slightly better in the seas and oceans (Fig. 2a) than on land. Numerous species range shifts under contemporary climate change have been documented not only in the Northern Hemisphere and especially in the North Sea (Beare et al. 2004, Simpson et al. 2011, Pitois et al. 2012) and the Bering Sea (Orensanz et al. 2004, Overland and
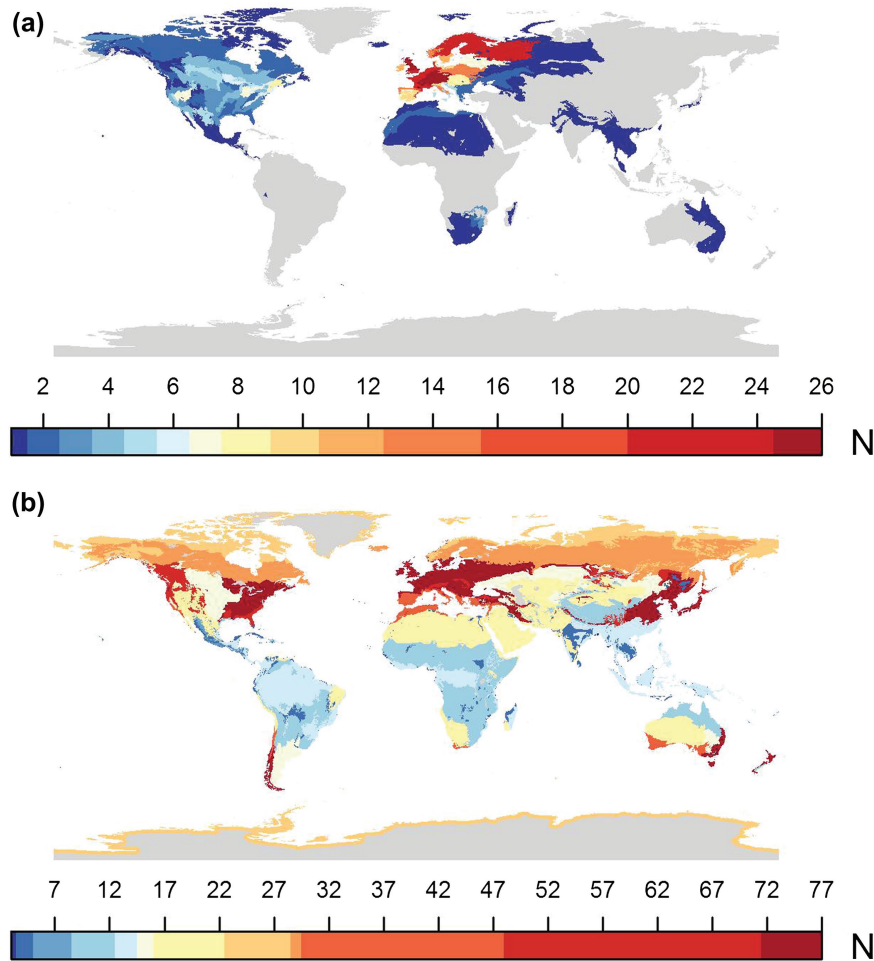
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Figure 1. Global maps of research effort on climate-related range shifts since 1850s for terrestrial ecosystems. Total number of publications (N) is reported for each of the terrestrial ecoregions (a) and biomes (b) of the World. See global maps of the World Wildlife Fund's (WWF) for a detailed delineation of each of the terrestrial ecoregions and biomes of the World (Olson et al. 2001, Spalding et al. 2007).

Stabeno 2004), but also in the Southern Hemisphere, although here chiefly in the Tasmanian Sea (Last et al. 2011, Wernberg et al. 2011, Przeslawski et al. 2012). As on land, tropical areas such as the Eastern Indo-Pacific and Tropical Eastern Pacific realms are proportionally understudied (Fig. 2b).

Taxonomic shortfalls

Most studies reporting climate-related range shifts have focused on terrestrial animals (n = 89), whereas we found especially few studies on marine plants (n = 8) (Table 1). Thus, in the seas and oceans the ratio between studies focusing on plants (9%) and studies focusing on animals (91%) was strongly unbalanced. Although more balanced on land, we also found a trend towards more reports for animals (72%) than for plants (28%). This bias in the research effort between animals and plants was strongly significant (Pearson's Chi-squared test with Yates' continuity correction: Chi-squared = 10.16, DF = 1, p-value = 0.001).

Methodological shortfalls

Studies reporting changes in species distribution under contemporary climate change have focused primarily on

latitudinal or elevational/bathymetric range shifts (Table 1 and Fig. 3a). We found five times as many studies focusing on latitudinal range shifts (n = 95) and three times as many studies focusing on elevational/bathymetric range shifts (n = 57) as studies focusing on longitudinal range shifts (n = 20) (Table 1). The first axis of the constrained correspondence analysis (CCA) accounted for 65% of the total variation and clearly separated studies focusing on latitudinal range shifts (negative values) from those

Table 1. Number of publications reporting climate-related changes in the distribution of plant and animal species across terrestrial and marine ecosystems for each of the seven studied distribution parameters: longitude (LON); latitude (LAT); elevation/depth (E/D); leading edge (LE); trailing edge (TE); optimum (O); and abundance (A).

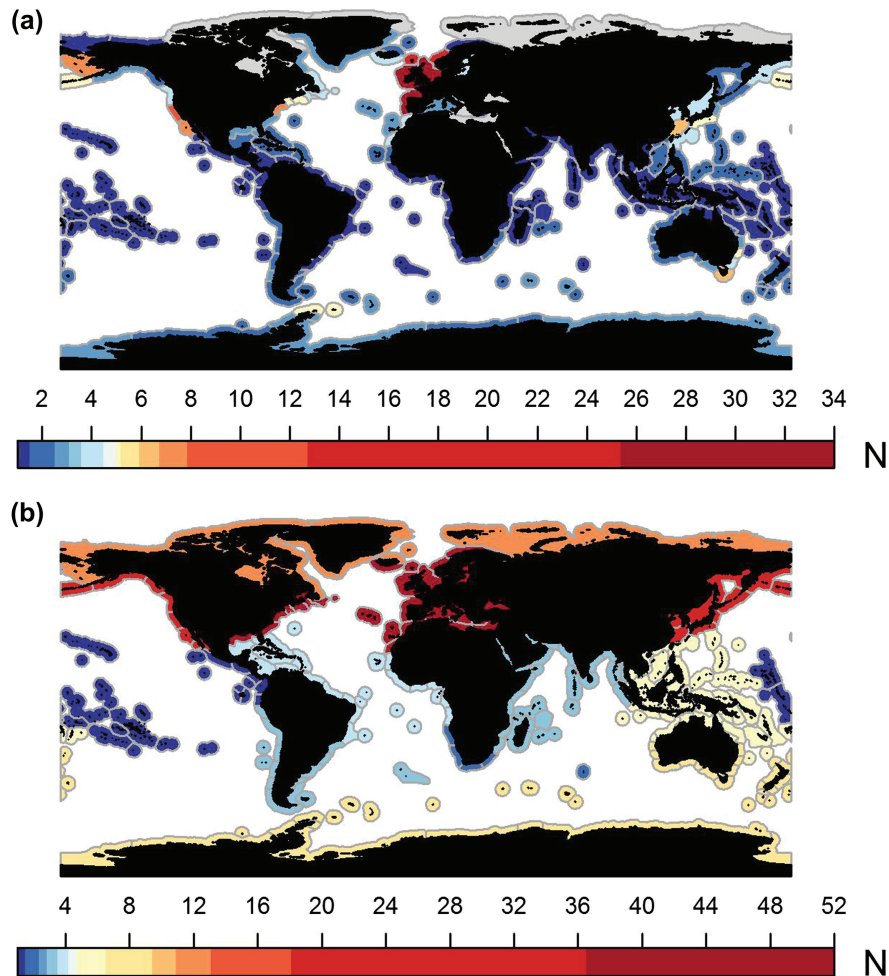|	Terrestrial		Marine	
	Plants	Animals	Plants	Animals
LON	1	8	2	9
LAT	3	44	5	43
E/D	24	26	1	6
LE	19	57	2	35
TE	11	41	4	25
O	12	27	0	16
A	15	44	5	64

Figure 2. Global maps of research effort on climate-related range shifts from 1850s onwards for marine ecosystems. Total number of publications (N) is reported for each of the marine ecoregions (a) and realms (b) of the World. See global maps of the World Wildlife Fund's (WWF) for a detailed delineation of each of the marine ecoregions and realms of the World (Olson et al. 2001, Spalding et al. 2007).

focusing on elevational/bathymetic range shifts (positive values) (Fig. 3a). Only ten studies focused on both latitudinal and elevational/bathymetric range shifts simultaneously (Hill et al. 2002, Perry et al. 2005, Franco et al. 2006, Hickling et al. 2006, Nye et al. 2009, Zuckerberg et al. 2009, Engelhard et al. 2011, Comte and Grenouillet 2013, Pinsky et al. 2013, Hernández et al. 2014). Importantly, we are aware of only three studies so far that have reported changes in species distributions by specifically focusing on latitude, longitude and elevation or depth simultaneously (Engelhard et al. 2011, Comte and Grenouillet 2013, Pinsky et al. 2013).

Latitudinal range shifts have been almost exclusively documented within the animal kingdom, with a limited number of cases for plants (Table 1). Additionally, we found that publications treating latitudinal range shifts have focused primarily on changes at the distributional margins (shifts or abundance changes at the leading and trailing edges) rather than on changes within the distribution (shifts or abundance changes at the optimum position) (Fig. 3a). For animals, there is clear evidence of poleward range shifts documented through either expansion at the leading edge (Parmesan et al. 1999, Thomas and Lennon 1999, Hickling et al. 2005, Pitt et al. 2010, Brommer et al. 2012, Moreno-Rueda et al.

2012), retraction at the trailing edge (Parmesan et al. 1999, Thomas and Lennon 1999, Franco et al. 2006, Zuckerberg et al. 2009, Brommer et al. 2012), increasing abundance at the leading edge (Sagarin et al. 1999, Myers et al. 2009, Jiguet et al. 2010, Simpson et al. 2011, Breed et al. 2013) or decreasing abundance at the trailing edge (Sagarin et al. 1999, Rogers-Bennett 2007, Myers et al. 2009, Jiguet et al. 2010, Breed et al. 2013). The relatively few studies on range shifts or abundance changes at the core of animal distributions have found similar trends (Engelhard et al. 2011, Mattila et al. 2011, Lehikoinen et al. 2013). For plants, reports on latitudinal range shifts are very scarce (n = 8) (Table 1) and show striking differences between the terrestrial and marine ecosystems (Fig. 3b). Among the 42 studies focusing on plants, the proportion of publications treating latitudinal range shifts was much higher in the seas and oceans (63%) than on land (9%). However, latitudinal range shifts for marine plants did not show clear patterns (Lima et al. 2007, Wernberg et al. 2011, Tanaka et al. 2012). For instance, the northern range limits of southern macroalgae (the trailing edge) along the eastern and western coasts of Australia shifted southward (Wernberg et al. 2011) whereas the southern range limits of northern algae (also trailing edge) along the eastern coast of
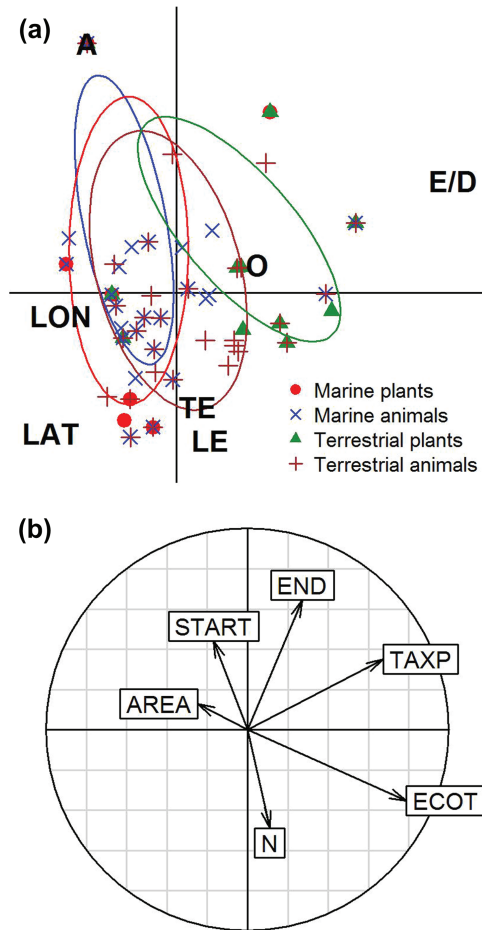
Figure 3. Biplot (a) and correlation circle (b) from the constrained correspondence analysis (CCA) based on the matrix (Supplementary material Appendix 2, Table A2) of publications (n = 212) reporting climate-related range shifts since 1850s and focusing on at least one of the seven distribution parameters studied in our review: longitude (LON), latitude (LAT), elevation/depth (E/D), leading edge (LE), trailing edge (TE), optimum (O) and abundance (A). The first- and second-CCA axes account for 65 and 17% of the total inertia, respectively. Explanatory variables used as constraints in the CCA are ecosystem (ECO), kingdom (TAX), total number of studied taxa (N), total surface area (AREA), starting year (START) and ending year (END). ECOT and TAXP, which are strongly correlated with the first-CCA axis, indicate studies focusing on terrestrial ecosystems and plants, respectively.

Portugal remained stable (Lima et al. 2007). For terrestrial plants, only a few poleward range shifts have been reported (Lesica and McCune 2004, Groom 2013, Hernández et al. 2014), and the fingerprint of climate change is not evident (Groom 2013).

Vertical range shifts have been reported principally on land. Marine bathymetric range shifts of potentially equal importance remain widely understudied (Table 1 and Fig. 3a), though some reports exist for a limited number of taxa (Perry et al. 2005, Dulvy et al. 2008, Nye et al. 2009, Tunin-Ley et al. 2009, Engelhard et al. 2011, Harley 2011, Pinsky et al. 2013). For terrestrial ecosystems, nearly as many elevational range shifts have been reported for plants as for animals (Table 1) with elevation being the most commonly used geographical gradient to detect

species range shifts amongst studies focusing on terrestrial plants (Fig. 3a). Additionally, we found that reports studying elevational range shifts have mostly focused on changes within the core of the distribution, rather than on changes at the distributional margins (Fig. 3a). For terrestrial plants and animals, elevational range shifts at the core of the distribution show consistent results with a clear upward trend (Konvicka et al. 2003, Lenoir et al. 2008, Raxworthy et al. 2008, Bergamini et al. 2009, Chen et al. 2009, Popy et al. 2010, Comte and Grenouillet 2013). Elevational range shifts at the distributional margins, however, show divergent patterns for terrestrial animals and terrestrial plants. For terrestrial animals, both the leading and the trailing edges seem to be responsive and upward shifts have been documented at both edges (Konvicka et al. 2003, Wilson et al. 2005, Moritz et al. 2008, Raxworthy et al. 2008, Ploquin et al. 2013). For terrestrial plants, however, the trailing edge seems to be less responsive than the leading edge (Brusca et al. 2013). Among studies focusing on the leading edge of terrestrial plants' elevational distribution (n = 19), 79% have found a similar trend towards upwards shifts (Parolo and Rossi 2008, Bergamini et al. 2009, Frei et al. 2010, Felde et al. 2012, Jump et al. 2012, Telwala et al. 2013). In contrast, the few studies focusing on the trailing edge of terrestrial plants' elevational distribution (n = 10) have found divergent results, with either a clear upward trend (Brusca et al. 2013, Telwala et al. 2013, Kopp and Cleland 2014) or no trend (Bergamini et al. 2009, Frei et al. 2010).

A working agenda for studying climate-related range shifts

Based on the geographic, taxonomic and methodological shortfalls discussed above, we propose a working agenda for future studies by pointing to where, what and how we should be looking next to improve our general knowledge of climate-related range shifts.

Wanted: investigation of distribution changes in tropical lowlands and tropical waters

Although the number of reports on range shifts has increased almost exponentially over the last three decades, more research efforts are still needed at low latitudes and especially within the tropical zone, the most species-rich part of the World and the area hosting most threatened taxa. For terrestrial ecosystems, evidence of recent species range shifts in the tropics has mostly come from studies in mountainous regions (Pounds et al. 1999, Raxworthy et al. 2008, Chen et al. 2009, Feeley et al. 2011, Harris et al. 2012, Angelo and Daehler 2013, Siraj et al. 2014, Freeman and Freeman in press) where biotic responses seem to match local temperature increases significantly more closely than in temperate-zone mountains (Freeman and Freeman in press). In contrast, evidence for latitudinal or longitudinal range shifts in the lowland tropics is almost inexistent (but see Maranz 2009). Yet, species (especially ectotherms, including plants) may be more vulnerable in these regions because they are likely to be closer to their physiologically constrained upper thermal tolerance limits (Deutsch et al. 2008, Kellermann

et al. 2012, Sunday et al. in press). Note that if most terrestrial ectotherms have a limited physiological thermal-safety margin, they may still rely on behavioural plasticity by using shade, burrows or evaporative cooling to avoid overheating and survive climate warming in the lowland tropics (Sunday et al. in press). This fact might potentially explain the absence of range shift reports for terrestrial ectotherms in the lowland tropics. However, such thermoregulatory behaviour does not exist for tropical lowland plants. Therefore, tropical lowland biotas, especially plants, should become a priority in global change research since there are no species source pools now living in hotter places that are available to replace climatically displaced or declining species in tropical lowland ecosystems, potentially leading to tropical lowland biotic attrition (Colwell et al. 2008, Feeley and Silman 2010), with unknown consequences for ecosystem functioning.

For marine ecosystems, evidence of recent species range shifts in tropical waters is even scarcer, with at most a handful of reports (Precht and Aronson 2004, Rivadeneira and Fernández 2005, Poloczanska et al. 2011). Still, for the same reasons as for terrestrial ecosystems, biotic attrition is more likely in tropical waters than in temperate or arctic waters. Additionally, equatorward range margins of marine ectotherms have been reported to be more at equilibrium with their heat tolerances than equatorward range margins of terrestrial ectotherms, which have been reported to lag in response to climate warming (Sunday et al. 2012). Considering this fact, marine ectotherms should be more sensitive to climate warming than terrestrial ectotherms, suggesting that biotic attrition may happen first in tropical waters. However, detection of climate-related range shifts in tropical ecosystems is even more challenging than elsewhere on Earth because long-term data are often scarce for tropical organisms (Feeley 2012).

Wanted: investigation of lowland range shifts of terrestrial plants

Even when long-term data are available, as for Europe, the detection of lowland range shifts remains rare for terrestrial plants, especially woody plants (Jump et al. 2009). Yet, two very recent studies have confirmed that poleward range shifts of terrestrial plants, including woody plants, are already happening (Groom 2013, Cavanaugh et al. in press). Notably, Cavanaugh et al. (in press) have found evidence for a threshold response, with declining frequency of severe cold winter events allowing for poleward expansion of mangroves at the northern end of their historic range on the east coast of Florida. Therefore, for terrestrial plants, the apparent lack of lowland range shifts could to some extent be due to a lack of research effort rather than a true absence of shifts (Jump et al. 2009). Nevertheless, the combined effect of high persistence capacities and poor dispersal abilities of long-lived perennial herbs and woody plants, as well as the lack of nearby source areas in lowlands, which constrains the ability of terrestrial plants to colonize and establish outside their lowland ranges, probably limit climate-change-driven lowland range shifts in many plants, leading to lagged responses (Bertrand et al. 2011, Svenning and Sandel 2013).

Interestingly, in their meta-analyses Chen et al. (2011) found that the observed latitudinal range shifts under contemporary climate change match the expected ones given global temperature increase. However, contrary to their meta-analysis on elevational range shifts, their meta-analysis on latitudinal range shifts did not incorporate plants, but only animals (i.e. birds, mammals, arthropods, herptiles, fish and molluscs) and chiefly the most vagile groups like birds, butterflies, dragonflies and damselflies. For these reasons, and because plants may particularly challenge this result, given the above-mentioned arguments, we cannot agree with the authors' conclusion that latitudinal range shifts are not consistently lagging behind climate (Bertrand et al. 2011, Devictor et al. 2012). Instead, we call for more research efforts on distribution changes of lowland plant ranges before drawing general conclusions on such lag effects.

Wanted: investigation of bathymetric range shifts for marine plants

There are relatively few studies reporting bathymetric range shifts under contemporary climate change, especially for plants (but see Tunin-Ley et al. 2009). For marine animals, bathymetric range shifts have already been reported for both shallow-water and deep-sea animals penetrating greater depths as sea temperature rises (Perry et al. 2005, Dulvy et al. 2008, Nye et al. 2009, Engelhard et al. 2011, Harley 2011, Pinsky et al. 2013). For marine photosynthetic groups, such as phytoplankton and macroalgae, however, expectations of bathymetric range shifts towards greater depths are not so straightforward due to the obvious physiological constraint for light that becomes a limiting factor in deep water (Micheli et al. 2008), but such hypotheses remain to be tested. Looking at the temporal distribution of 20 *Ceratium* species in the Mediterranean Sea over the last century, Tunin-Ley et al. (2009) have showed a progressive disappearance from the surface layer of likely stenothermic species, suggesting range retractions towards greater depths in response to water warming. Although several studies reported global changes in marine phytoplankton biomass and community structure during the 20th century (Reid et al. 1998, Richardson and Schoeman 2004, Hays et al. 2005, Boyce et al. 2010, Pitois et al. 2012, Suikkanen et al. 2013), little evidence of distribution or abundance changes has been reported at the species level (Edwards et al. 2006, Henriksen 2009, Tunin-Ley et al. 2009, Wiltshire et al. 2010), with only a single study reporting bathymetric range shifts (Tunin-Ley et al. 2009). Yet, these ubiquitous microscopic and phototrophic organisms account for approximately half the production of organic matter on Earth (Field et al. 1998) and are at the bottom of the pelagic food chain and thus likely to affect the abundance and diversity of marine organisms in higher trophic levels (Beaugrand et al. 2003, Richardson and Schoeman 2004). For this reason and to better understand observed climate-related range shifts throughout the higher trophic levels of the pelagic food chain (Last et al. 2011, Simpson et al. 2011, Worm and Tittensor 2011), we urge more research focusing on bathymetric range shifts of marine plants.

Wanted: investigation of distribution changes of prokaryotes

Climate-related range shifts of prokaryotic organisms (bacteria and archaea) are understudied in both marine and terrestrial ecosystems, though these microorganisms are among the most abundant and perhaps also the most diverse organisms on Earth (Whitman et al. 1998). The lack of microbial studies probably stems from our ignorance of the patterns and determinants of microbial distribution within and between Earth's major biomes (Nemergut et al. 2011) with the biogeography of microorganisms still a relatively young science compared to the biogeography of macroorganisms (Martiny et al. 2006).

Wanted: use of multi-facetted approaches for more comprehensive assessments

Despite the remarkable number of studies documenting species range shifts under contemporary climate change, only 10% have used a multidimensional approach focusing on at least two geographical dimensions (e.g. latitude and elevation) simultaneously to assess distribution shifts or abundance changes either at the leading edge, the trailing edge or the optimum position (Jepsen et al. 2008, Engelhard et al. 2011, Mattila et al. 2011, Groom 2013, Pinsky et al. 2013). We are aware of only a single study using a multi-facetted approach that simultaneously assesses changes across three distribution parameters (leading edge, trailing edge and optimum) and along all three geographical gradients (latitude, longitude and elevation). In that study, Comte and Grenouillet (2013) examined the distributional changes of 32 stream fish species in France between 1980–1992 and 2003–2009. They found, on average, that stream fish species shifted their ranges to higher elevations by means of leading-edge expansions and horizontally (e.g. latitude and longitude) by means of trailing-edge retractions. Conducting comprehensive, multi-facetted assessments of species range shifts and using the results for understanding geographical patterns in climate-related range shifts (Grenouillet and Comte in press) is a real challenge that has yet to be taken up, but which should be an important future research objective, providing a better basis for forecasting biodiversity responses to future climate change.

Wanted: use of local climate velocities to improve expectations for biological shifts

Another looming challenge that a handful of studies have already taken up is to contrast observed species range shifts with those expected from climate change measures that account for the potentially complex mosaic of local climate changes (Comte and Grenouillet 2013, Pinsky et al. 2013, Poloczanska et al. 2013). Climate change velocity metrics (Loarie et al. 2009, Burrows et al. 2011) describe the pace and direction of local climate change with the option to incorporate both temperature and precipitation changes simultaneously thus providing improved expectations for biological shifts (Tingley et al. 2012, Pinsky et al. 2013, Poloczanska et al. 2013, VanDerWal et al. 2013) compared to expectations based uniquely on global trends in temperature changes (Chen et al. 2011). Pinsky et al. (2013) have already demonstrated that marine fish and invertebrate species from the continental shelves of North America closely tracked local differences in climate velocity that explained the magnitude and direction of shifts, including seemingly inconsistent range shifts (Lenoir et al. 2010), more efficiently than did biological differences among species. On the contrary, by contrasting the observed elevational and upstream-downstream range shifts with the expected ones given the velocity of climate change along the reaches of the hydrographic network in France, Comte and Grenouillet (2013) have shown that the majority of stream fish species did not shift at a pace sufficient to track changing climate, but are lagging far behind expectations. This discrepancy between marine and terrestrial taxa supports the idea that marine taxa may be better able to keep pace with climate change than terrestrial taxa because marine taxa have higher rates of propagule production and dispersal by ocean currents, fewer barriers to dispersal and consequently higher filling of their thermal niches (Sunday et al. 2012). Such an understanding of the mosaics of local climate changes is crucial for determining when observed range shifts may jeopardize the survival of a species or local population.

A framework linking range shift to extinction risk

Based on the unified classification of geographical patterns of species range shifts described below, we propose to position observed and expected range shifts in a bi-dimensional space defined by persistence and movement processes, which are both related to extinction risks. We then discuss the relative positions of species in this bi-dimensional space in light of their ecological traits to lead to more informed assessments of extinction risks. Because ecological traits have been found to have little explanatory power to predict observed species movements (Angert et al. 2011), simply linking ecological traits to movement processes is not enough. Indeed, other facets of range shifts, such as persistence, have to be brought into the picture to illuminate geographical patterns of species range shifts (Dullinger et al. 2012, Grenouillet and Comte in press). For this reason, we here advocate the use of such a bi-dimensional space to account for both persistence and movement processes when linking species range shifts to their ecological traits to improve predictions of extinction risks.

Categorizing geographical patterns of species range shifts under climate change

Recently, Maggini et al. (2011) laid out an exhaustive catalog of all the possible geographical patterns of species range shifts under contemporary climate change: (*a*) leading-edge expansion; (*b*) trailing-edge retraction; (*c*) dispersal-driven expansion that is normally contained by exogenous factors; (*d*) optimum shift; (*e*) range expansion; (*f*) range retraction; (*g*) complete shift of the distribution; and (*h*) change in abundance. More generally, Breshears et al. (2008) distinguished three principal categories of species range shifts as

climate warms: (*a*) march; (*b*) lean; and (*c*) crash. March range shifts represent the most dynamic category of range shifts, with colonization events at the leading edge and local extinction events at the trailing edge, leading not just to range margin displacements, but usually also to shifts in the optimum position within the existing range. Lean range shifts involve stable edges with the optimum shifting within the existing range. Crash range shifts involve stable edges and a stable optimum, but overall abundance declines across the existing range. Hence, changes occurring within the ranges of species without changes in range margins (crash and lean) do not have the same ecological and evolutionary consequences as when changes occurring within the ranges of species are linked to shifts at the range margins (march) (Lenoir and Svenning 2013). Intrinsically, crash and lean range shifts both suggest stronger dispersal limitation (Svenning and Sandel 2013) than march range shifts.

Combining the exhaustive catalogue from Maggini et al. (2011) together with the broad classification from Breshears et al. (2008), we distinguished five broad categories of species distribution changes, namely those involving: (*a''*) colonization and establishment events within the existing range (lean); (*b''*) extinction events within the existing range (retract); (*c''*) colonization and establishment events inside and outside the existing range (expand); (*d''*) scenario *b''* plus *c''* (march); and (*e''*) overall abundance declines across the existing range (crash). We chose to distinguish between pure range expansions, pure range retractions and the combination of both (march range shifts), because each has different ecological and evolutionary consequences. For instance, both expand and march range shifts require the ability for species to move outside their existing range throughout colonization and establishment events at the leading edge, but pure range expansions also involve the ability for species to persist locally at the trailing edge.

Persistence and movement as key processes in range shifts

Persistence and movement are two important means by which species cope with climate change and avoid extinction. Species may either show: 1) a high persistence rate and a high movement rate (expand); 2) a low persistence rate and a low movement rate (retract); 3) a low persistence rate, but a high movement rate (march); or 4) a high persistence rate, but a low movement rate (lean). Based on species' persistence rate (SPR) and species' movement rate (SMR), we arranged the lean, retract, expand and march range shifts within a bi-dimensional space defined by SPR and SMR (Fig. 4). SMR can be assessed by computing, for instance, the area of newly suitable habitats where the species colonized and established successfully outside and within its former existing range (i.e. leading-edge dynamics involving colonization and establishment events: orange hatching in Fig. 4). In contrast, SPR can be assessed by computing, for example, the area of formerly suitable habitats where the species remained present despite habitat conditions becoming unsuitable given expectations based on the velocity of local climate changes (i.e. trailing-edge disequilibrium dynamics involving delayed local extinctions: violet hatching in Fig. 4). Although the computation

of SMR requires only data on observed range shifts, the computation of SPR also requires data on expected range shifts, given the velocity and directionality of local climate changes. Crash range shifts do not involve movements but a high persistence rate and thus can also be added to the bi-dimensional space defined by SPR and SMR (Fig. 4). Of course, these broad categories are not mutually exclusive and can be combined to develop all possible patterns of range shifts as climate changes.

Expanding and marching species are less prone to extinction

Species expanding their range as climate warms are the least prone to extinction and can even be considered as winners (Fig. 4). For instance, in Great Britain, vagile endotherms like birds have been reported to shift northward at their leading edge, but also persist at their trailing edge, thus realizing an overall northward range expansion of their range in the Northern Hemisphere (Thomas and Lennon 1999). In general, vagile, long-lived and large-sized organisms are likely to colonize and establish outside their existing range as well as persist locally. To a lesser extent, species exhibiting march range shifts under contemporary climate change are also less prone to extinction (Fig. 4). For instance, in the Northern Hemisphere, vagile, short-lived and small-sized ectotherms like butterflies have been reported to shift northward at both their leading and trailing edges (Parmesan et al. 1999). Similarly, marine ectotherms, which more fully occupy the extent of latitudes tolerable within their thermal tolerance limits, have been shown to expand at their poleward range margins and contract at their equatorward range margins (Sunday et al. 2012). In general, vagile, short-lived and small-sized species for which colonization, establishment and extinction events occur on a relatively short time scale (high generation turnover) are likely to conform to march range shifts and thus be less prone to extinction.

Retracting and crashing species are most at risk of extinction

Dispersal barriers or 'climatic traps', such as small mountain ranges with a limited elevational gradient may spatially constrain species range shifts towards summits and prevent vagile, short-lived and small-sized ectotherms like butterflies from shifting their leading edges to higher latitudes, thus leading to elevational range retractions (Wilson et al. 2005) and ultimately to latitudinal range retractions as climate warms. Non-vagile, short-lived and small-sized species are even more likely to retract their ranges as climate changes. The most striking evidence of such range-shift retractions involving extinction processes or abundance declines at one or both margins come from non-vagile and thermo-sensitive ectotherms like lizards and amphibians (Pounds et al. 1999, Whitfield et al. 2007, McMenamin et al. 2008, Sinervo et al. 2010). Range retractions, if combined with overall abundance declines across the existing range (i.e. crash) increase the risk of extinction and may ultimately lead to the total disappearance of a given species (Fig. 4). Similarly, rare or endemic species having a restricted distribution for which
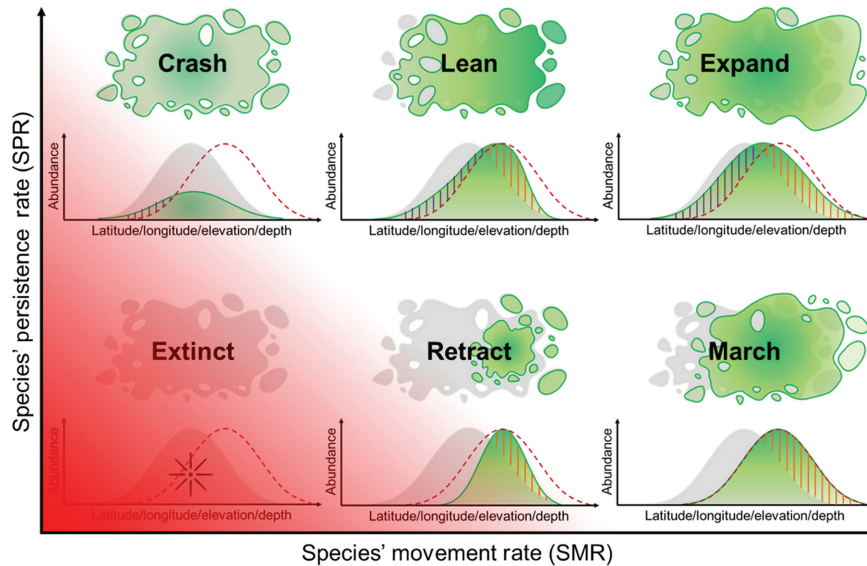
Figure 4. Conceptual representations of several types of species range shifts grouped into five broad categories (march, expand, retract, lean and crash) and their positions in a bi-dimensional space defined by species' persistence rate (SPR) and species' movement rate (SMR). Grey-shaded response curves along a given geographic gradient (latitude, longitude or elevation/depth) represent a species' range before climate change. Overlying transparent and greenish response curves represent the observed species' range after a period of climate change (whether or not change is still ongoing). Dotted and red response curves represent the expected species' range under a simplistic assumption involving only temperature increase. Note that more advanced and realistic expectations can be drawn by using the observed velocity of local climate changes. Violet and orange hatching represent persistence and movement processes, respectively. For simplicity, we represent only positive patterns towards higher latitudes, longitudes, elevations or towards greater depths in the ocean. But negative patterns, towards lower latitudes, longitudes, elevations or towards shallower depths in the ocean as well as expanding and retracting patterns at both range margins could also be added to the bi-dimensional space. Not all of these specific types of range shifts are mutually exclusive. Some can be combined to develop many possible patterns of range shifts.

the degree of climate warming far exceeds their ability to shift towards suitable conditions due to dispersal limitation, e.g. due to natural or anthropogenic habitat fragmentation, are likely to be prone to extinction through a combination of range retractions and overall abundance declines throughout their existing range (Morueta-Holme et al. 2010). Endemic species restricted to low and isolated mountains in the temperate and tropical zones are especially threatened with extinction as a consequence of range-shift retractions (Dullinger et al. 2012).

The intermediate case of leaning species

The case of species exhibiting lean range shifts under contemporary climate change is not alarming, in terms of extinction risks, unless it involves transient responses. For instance, sessile, long-lived and large-sized trees for which colonization, establishment and extinction events occur on a much longer time scale than the usual period of observation (low generation turnover) have been shown to sometimes persist after climate has turned unsuitable for sexual reproduction within their existing range without colonizing and establishing outside, thus exhibiting lean range shifts (Kelly and Goulden 2008). This response, however, might be transient and might correspond to early stages of a full shifting process lagging behind climate change as a kind of climatic debt (Dullinger et al. 2012), in the sense of a species being out of equilibrium with climate as a consequence

of delayed biotic responses. Trees may be particularly prone to be in disequilibrium with climate and to pay off their climatic debts by abrupt range shifts involving widespread forest dieback, if critical thresholds are crossed after long-term climatic changes, extreme climatic events or climate-induced pest outbreaks (Mantgem et al. 2009, Carnicer et al. 2011). In general, vegetation disequilibrium with climate is likely to be prevalent over the next 50–200 yr, with leading-edge disequilibrium dynamics due to lags in colonization and establishment and trailing-edge disequilibrium dynamics involving delayed local extinctions (Svenning and Sandel 2013). However, such delayed responses and disequilibrium dynamics are not specific to the plant kingdom. Marine fishes with larger body sizes, slower maturation and larger sizes at maturity are also lagging behind climate change compared to marine fishes with smaller body sizes, faster maturation and smaller sizes at maturity (Perry et al. 2005). Similarly, the climatic debt accumulated by birds over two decades (1990–2008) in Europe, corresponding to a 212-km lag behind climate change, is much larger than for butterflies, which have small body sizes and short life spans compared to birds (Devictor et al. 2012). The complexity of these lagged responses is a major challenge to take into consideration when assessing species' extinctions risks. Indeed, species exhibiting lean range shifts are seemingly less prone to extinction than species exhibiting range retractions (Fig. 4), but as soon as the climatic debt has to be paid off, these species are likely to undergo abrupt range declines and be under high risks of extinction. As a potential example, the small-range tree

species *Torreya taxifolia* has experienced range-wide decline, suggested to be a lagged response to climate change (Barlow and Martin 2005).

Conclusion

Recent deviations from simple uni-dimensional and uni-directional range shifts involve complex drivers, such as mosaics of local climate change, which need to be studied using multi-facetted approaches to properly assess species' movement rate (SMR). These multi-facetted approaches should be combined with the use of contrasts between observed and expected species range shifts, given the velocity of climate change, to estimate species' persistence rate (SPR). Positioning SMR and SPR into the bi-dimensional persistence rate vs movement rate space should further improve our abilities to assess extinction risks and provide managers with more tailored habitat- or species-management strategies for biodiversity conservation. To fill current research gaps, investigations of: 1) distribution changes in tropical lowland biotas; 2) lowland range shifts of terrestrial plants; 3) bathymetric range shifts of marine plants; or 4) distribution changes of prokaryotes would be particularly welcome, allowing the development of improved predictive models of future range shifts and species extinction risks.

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