



# Bioclimatic velocity: the pace of species exposure to climate change

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## ABSTRACT

**Aim** To investigate the velocity of species-specific exposure to climate change for mid- and late 21st century and develop metrics that quantify exposure to climate change over space and time.

**Location** California Floristic Province, south-western USA.

**Methods** Occurrences from presence/absence inventories of eight Californian endemic tree species (*Pinus balfouriana* [Grev.&Balf.], *Pinus coulteri* [D.Don], *Pinus muricata* [D.Don.], *Pinus sabiniana* [D.Don], *Quercus douglasii* [Hook.&Arn.], *Quercus engelmannii* [Greene], *Quercus lobata* [Nee] and *Quercus wislizeni* [A.DC.]) were used to develop eight species distribution models (SDMs) for each species with the BIOMOD platform, and this ensemble was used to construct current suitability maps and future projections based on two global circulation models in two time periods [mid-century: 2041–2070 and late century (LC): 2071–2100]. From the resulting current and future suitability maps, we calculated a bioclimatic velocity as the ratio of temporal gradient to spatial gradient. We developed and compared eight metrics of temporal exposure to climate change for mid- and LC for each species.

**Results** The velocity of species exposure to climate change varies across species and time periods, even for similarly distributed species. We find weak support among the species analysed for higher velocities in exposure to climate change towards the end of the 21st century, coinciding with harsher conditions. The variation in the pace of exposure was greater among species than for climate projections considered.

**Main conclusions** The pace of climate change exposure varies depending on period of analysis, species and the spatial extent of conservation decisions (potential ranges versus current distributions). Translating physical climatic space into a biotic climatic space helps informing conservation decisions in a given time frame. However, the influence of spatial and temporal resolution on modelled species distributions needs further consideration in order to better characterize the dynamics of exposure and species-specific velocities.

## Keywords

California, climate change velocity, exposure, range dynamics, species distribution models, temporal dynamics, vulnerability.

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## INTRODUCTION

Assessing vulnerability of terrestrial biodiversity to climate change over the next 50–100 years is a highly uncertain and complex task. Species distribution modelling (SDM) is the most widespread technique used to assess species exposure to future climate change impacts (e.g. Thomas *et al.*, 2004;

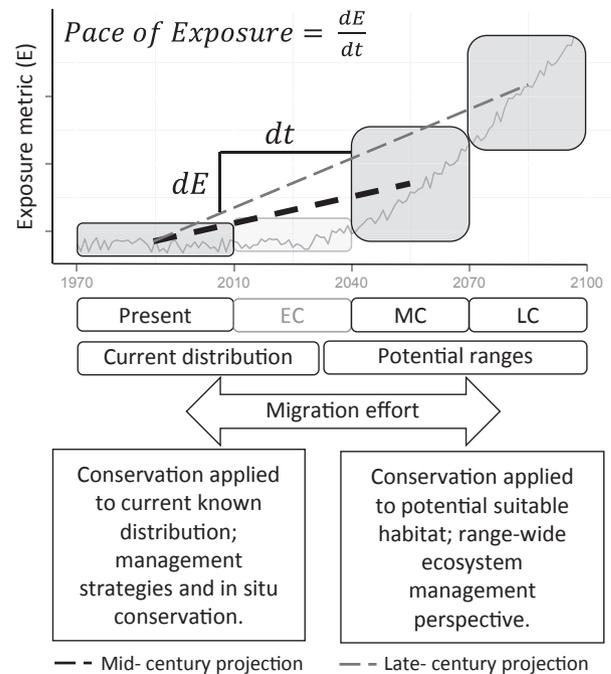
Thuiller, 2004; Araújo *et al.*, 2011). In other words, SDMs are able to picture the extent of climate change likely to be experienced by a species ('exposure' *sensu* Dawson *et al.*, 2011). SDM relates species presence or abundance to climate and other environmental variables, typically using statistical learning methods, so that the bioclimatic profile of the species is quantified (Franklin, 2010a). The model can then

be projected to mapped scenarios of future climate to evaluate which areas will be more or less climatically suitable for the species relative to present conditions.

A recent line of research has focused on developing methods to measure how far climate conditions might shift in space during a particular interval of time, given that any species' survival will depend in part on its ability to track geographical shifts in suitable climatic conditions (Loarie *et al.*, 2009; Ackerly *et al.*, 2010; Burrows *et al.*, 2011). Loarie *et al.* (2009) derived climate velocity ( $\text{km year}^{-1}$ ) by comparing grids of historic and projected future mean annual temperature. They calculated climate velocity at a location as the projected change in temperature per unit time ( $^{\circ}\text{C year}^{-1}$ ) divided by the local spatial gradient in temperature ( $^{\circ}\text{C km}^{-1}$ ). Loarie *et al.* (2009) used the measure to examine the patterns of climate exposure and conservation risk for the world's major biomes. In another study, Ackerly *et al.* (2010) mapped and analysed local climate change velocity in California to help identify the magnitude and pattern of biodiversity risk. Moreover, some studies suggest a link between the velocities of past climatic changes on species extinction and evolution (Nogués-Bravo *et al.*, 2010; Sandel *et al.*, 2011); therefore, it is important to detect high velocities under the rapid ongoing climatic warming, as species' capacities for adaptation and migration may be challenged (Davis & Shaw, 2001).

Presumably, climate velocity is proportional to the rate at which the biota of an area must migrate locally in order to remain in similar climate conditions as the regional climate changes. However, species distributions are rarely controlled by a single climate factor such as mean annual temperature and, as Ackerly *et al.* (2010) point out, species will likely manifest distinct, individualistic responses to climate change. Not only are responses species specific, but climate velocities will also vary regionally for the same species (e.g. Tingley *et al.*, 2012). Thus, while climate velocity is a useful concept, additional research is needed to incorporate other bioclimatic variables and to better understand how patterns of climate velocity vary between species and within the range of a species. Moving from physical climate space to a biotic climatic space could help guide the location and timing of conservation priorities and management actions for a given species (Hannah *et al.*, 2002; Mawdsley *et al.*, 2009) (Fig. 1).

In the present study, we apply the concept of climate velocity to SDMs calibrated for recent historical climate (1971–2000) and projected to climates for mid-century (MC; 2041–2070) and late century (LC; 2071–2100) to examine species-specific exposure to shifting climatic habitats. We analyse spatial patterns in the resulting maps of 'bioclimatic velocity' using a suite of spatio-temporal metrics that portray different aspects of the pace of species' exposure to climate change – that is, how quickly species become exposed to new climatic conditions. We include metrics that are useful for evaluating the potential for *in situ* conservation management as well as for *ex situ* management activities such as assisted migration or protection of areas that connect currently



**Figure 1** Framework for analysis of the velocity of species exposure (E) to climate change. Climatic periods are divided into three main time periods (t): early (2010–2040; EC)-, mid (2040–2070; MC)- and late (2070–2100; LC)-21st-century projections. The changes in the velocity can be analysed through changes in the slope between climatic periods (dashed lines, shown for mid-century and late century). This analysis can be applied to ranges and potential areas, current distributions or migrations metrics that link both types of metrics.

occupied areas to areas where bioclimatic conditions are projected to become favourable in future (Fig. 1).

We demonstrate our analytical framework for eight oak and pine species that are endemic to the California Floristic Province. We compare the pace of exposure to climate change among these species, which currently have similar distributions, and between MC and LC projections of climate change. Initially, we expected species to differ in their patterns of climate velocity for a given time period, but expected the differences to be slight given the high overlap in current distributions. We also expected that the pace of exposure would increase towards the end of the century given the harsher climatic conditions expected in California by 2100 with respect to 2050 (Cayan *et al.*, 2009).

## METHODS

### Study region and species occurrence data

The study region is the California Floristic Province, a biodiversity hotspot. This region has been determined to be one of the most sensitive biomes to climate change globally (Sala *et al.*, 2000; Underwood *et al.*, 2009) and therefore is an appropriate region to investigate bioclimatic velocities.

Our target species encompass eight species of oak and pine trees endemic to the California Floristic Province: *Pinus balfouriana* [Grev.&Balf.], *Pinus coulteri* [D.Don], *Pinus muricata* [D.Don.], *Pinus sabiniana* [D.Don], *Quercus douglasii* [Hook.&Arn.], *Quercus engelmannii* [Greene], *Quercus lobata* [Nee] and *Quercus wislizeni* [A.DC.]. These endemic species are dominant and widespread in the landscape, and therefore, they all play important roles in providing ecosystem services (carbon storage, wood production, wildlife habitat, etc.). Additionally, oaks woodlands are especially subject to conservation and sustainable development by the state (the California Legislature passed the Oak Woodland Conservation Act in 2001).

Species occurrence data were extracted from 42 existing vegetation inventories (compiled by Hannah *et al.*, 2008) comprising probabilistic and purposive sample designs. Only records from presence/absence vegetation surveys were used [*P. balfouriana* ( $n = 217$ ), *P. coulteri* ( $n = 323$ ), *P. muricata* ( $n = 65$ ), *P. sabiniana* ( $n = 2372$ ), *Q. douglasii* ( $n = 2422$ ), *Q. engelmannii* ( $n = 36$ ), *Q. lobata* ( $n = 699$ ) and *Q. wislizeni* ( $n = 2763$ )].

### Environmental data

Current climatic variables were obtained from a statistical downscaling (Flint & Flint, 2012) of the PRISM database (PRISM Climate Group, Oregon State University, available at: <http://prism.oregonstate.edu>) from 800-m to 270-m spatial resolution, including total annual precipitation, mean annual temperature, precipitation of the driest month, maximum temperature of the warmest month and minimum temperature of the coldest month. Although different species may be limited more or less by different subsets of these variables, we included all variables in the models to ensure maximum comparability among species and at the same time depict both averaged and extreme climatic ranges.

### Species distribution models and climate change projections

Using averaged climate data for the period 1971–2000, we estimated eight different SDMs for each species within the BIOMOD platform (Thuiller *et al.*, 2009; see Appendix S1 in Supporting Information for model descriptions) in order to obtain a robust measure of species climatic suitability based on model consensus (Araújo & New, 2007). Model calibration was undertaken with 70% of the presence/absence observations, and the remaining 30% were used for validation. We randomly selected 5000 absences from the many absences available for each species in the presence/absence dataset, allowing for a large number of absences covering the environmental space (Barbet-Massin *et al.*, 2012). In addition, each model was run twice using different random samples of absence to address potential sample bias in absences (Elith *et al.*, 2010).

In order to discriminate suitable from unsuitable areas, a threshold was applied to the continuous climatic suitability measure predicted by each SDM. We selected the threshold that maximized the true skill statistic (TSS) metric because this metric is unaffected by prevalence (Allouche *et al.*, 2006). Current and future suitable areas were then identified based on the agreement of at least five models in considering an area suitable after binary conversion using maximum TSS (committee averaging; see Gallien *et al.*, 2012 for details). A continuous consensus climatic suitability was then obtained for each grid cell by averaging the probabilities from those models agreeing with the consensus of suitable area. Although threshold choice may affect our results, major sources of uncertainty come from the choice of the statistical technique (Nenzén & Araújo, 2011). In our case, we have chosen an optimization threshold that balances correct prediction of presences and absences.

Habitat suitability dynamics were estimated based on differences between models' consensus projection for current climate and for future projected climate under the A2 emissions scenario using two global circulation models (GCMs): Geophysical Fluid Dynamics Laboratory (GFDL) and Parallel Climate Model (PCM). These GCMs were selected for climate change assessment in California because of their ability to reproduce historic climate patterns accurately (Cayan *et al.*, 2008). This combination of GCMs and scenario represents a 'strong change' scenario of a much warmer and drier California used by the California Climate Change Center for impact analysis (Cayan *et al.*, 2009) and to derive informed conservation policies. In order to assess potential differences in species exposure over time, two climate change periods were set: mid-21st-century (averaged climate 2041–2070; MC) and the late 21st century (averaged climate 2071–2100; LC). We did not perform early-century projections (2011–2040; Fig. 1) to avoid issues of temporal autocorrelation with historic climate.

### Bioclimatic velocity estimation

We computed the species' bioclimatic velocity of climate change using the same procedure as in Loarie *et al.* (2009), but applied to each species' suitability maps rather than to a single climate variable. We divided the temporal gradient (e.g. magnitude of change over time) of climate suitability by the spatial gradient (e.g. magnitude of change over space) in suitability for the period under analysis. The temporal gradient is computed as the difference in consensus probabilities between present and future projection per unit of time (years) for each map cell: 70 years for MC projection and 100 years for LC projection. Spatial gradients are computed for each map cell as the slope of probabilities using the maximum average technique (Burrough & McDonnell, 1998) in a 9-cell kernel (8-neighbour rule). To avoid infinite velocities, we excluded flat spatial gradients. The result is a velocity measure of the changes in climatic suitability of each species within its potential climatic range. Bioclimatic velocity has a

sign determined by the loss (negative) or gain (positive) in climatic suitability over time. However, the essence of the estimate is the same as for climate velocity *sensu* Loarie *et al.* (2009): combine local variation in suitable conditions (rather than in a given climatic variable) with the temporal gradient of change in suitable conditions. Bioclimatic velocity of each species was calculated as the average between the velocities based on each of the two GCMs for each period analysed.

### Dynamic exposure metrics

In order to evaluate how patterns of changing habitat suitability may affect different conservation strategies, we calculated several metrics that focus on the range level (referring to climatically suitable areas) and the population level (referring to current distributions of species within plots) (Fig. 1). Metrics are used to describe the pace of exposure to climate change and are based on bioclimatic velocity, potentially suitable areas and habitat suitability. Range-level metrics provide information most relevant to developing conservation strategies that address broad patterns of change in climate suitability, including potential new areas for colonization (whether assisted or not), whereas the population-level metrics inform more local management strategies focused on species' adaptation and *in situ* conservation (see Appendix S2 in Supporting Information for detailed description of the metrics). The estimates for each metric were derived from averaging values based on both GCMs in the period of analysis. In the case of high deviation from centrality, median values were used.

At the range level, five metrics were calculated:

(1) rate of species range change (SRC), which measures differences in potential suitable area gained and potential suitable area loss (Thuiller *et al.*, 2005) per unit of time (year) and is related to exposure to extinction due to rapid habitat loss; (2) rate of range exposure to migration (REM), calculated as the difference in suitable habitat area between full and null dispersal assumptions (Svenning & Skov, 2004; Araújo & New, 2007) divided by the time lapse between the current and targeted period, which emphasizes the importance of migration processes in lowering exposure; (3) range change velocity (RCV), which identifies potential impediments to tracking climate change at the edges of ranges, calculated as the net balance between trailing edge and leading edge bioclimatic velocity. Both trailing (suitable → unsuitable) and leading edges (unsuitable → suitable) were identified on a cell-by-cell basis using the consensus of SDMs on changes in suitability; (4) range spatial fragmentation (RSF), calculated as the number of discrete habitat patches gained or lost (McGarigal, 2013), and (5) range spatial aggregation (RSA), calculated as the percentage gain or loss of total suitable habitat occupied by the largest patch (McGarigal, 2013). These landscape structure metrics assess the spatial configuration of potential suitable habitat, which is related to population persistence (Opdam & Wascher, 2004).

To assess population-level exposure of current woodlands (e.g. the eight tree species are found in forests, open woodlands or savannas), we defined three metrics:

(1) Population migration exposure (PME), which measures the mean distance of plots containing the target species to projected future climatically suitable area using a least cost-distance route based on suitability measures. Skov & Svenning (2004) used a similar approach based on tree cover to assess potential migration routes for European herbs, and Wang *et al.* (2008) found a significant relationship between gene flow and a suitability resistance measure; (2) population climate-site exposure (PCE), calculated as the percentage of species plot locations switching from suitable to unsuitable conditions based on the set threshold of habitat suitability, divided by the time lapse between projections. Although this measure has been used as a surrogate for extinction risk (Thomas *et al.*, 2004), we have adopted it as a measure of woodland exposure risk to new climatic conditions; and (3) population climatic velocity (PCV), the mean bioclimatic velocity of species plots decreasing in suitability, calculated by overlaying woodland plots with the bioclimatic velocity grid computed using the methods described above.

We further performed hierarchical clustering in order to investigate the degree of similarity among species and projection times (MC and LC). First, we built a dissimilarity matrix using Mahalanobis multivariate distance and using the values for each metric as input variables. Subsequently, we calculated the clustering dendrogram using Ward's method of minimum variance among clusters.

## RESULTS

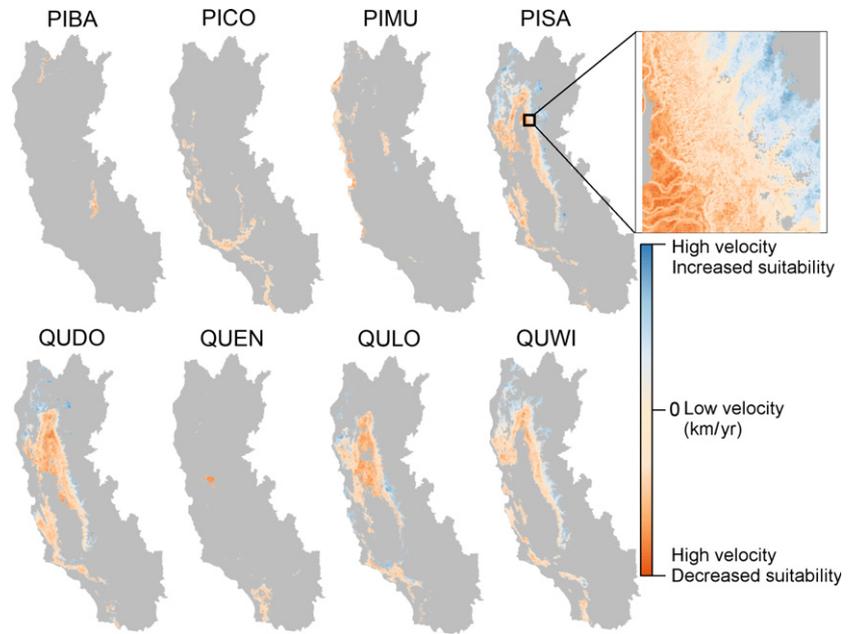
### Species distribution models accuracy

Species distribution models were able to reproduce current distributions with acceptable accuracy in discrimination capacity based on TSS (see Table S1 in Supporting Information). However, the accuracy varied between species (see Fig. S1 in Supporting Information), ranging from 0.65 TSS (*Q. lobata* and *P. muricata*) to 0.89 and 0.91 TSS (*P. balfouriana* and *Quercus sabiniana*, averaged values across models). For most species analysed, the range of accuracy values across models varied between 0.10 and 0.15. However, *P. muricata* exhibited a large range due to the poor fit of some models (flexible discriminant analysis and multiple adaptive regression splines). The difference between TSS values was greater across species than across models (see Fig. S1).

### Species bioclimatic velocity

Bioclimatic velocities vary greatly within each species potential range and in the climate change periods analysed (Fig. 2, Table 1). Mean values of bioclimatic velocity range between 0.11 and 0.32 km year<sup>-1</sup> depending on the species

**Figure 2** Averaged bioclimatic velocity of climate change for different California endemic tree species within their potential range, based on two global circulation models (GCMs) and eight species distribution models. (a) Bioclimatic velocity map for the period present (1971–2000) to late 21st century (2071–2100). Inset in Fig. 1 shows how different velocities may occur within relatively short geographical distances. PIBA = *Pinus balfouriana*, PICO = *Pinus coulteri*, PIMU = *Pinus muricata*, PISA = *Pinus sabiniana*, QUEN = *Quercus engelmannii*, QUDO = *Quercus douglasii*, QULO = *Quercus lobata*, QUWI = *Quercus wislizeni*.



**Table 1** Global circulation model-averaged bioclimatic velocities ( $\text{km year}^{-1}$ ) for species and time periods analysed. Values between brackets indicate 5% and 95% percentiles. Difference and Kendall correlation are between the climate periods.

	Mean bioclimatic velocity ( $\text{km year}^{-1}$ ) [5–95 percentiles]		Difference	Kendall correlation
	Mid-century	Late century		
<i>Pinus balfouriana</i>	0.21 [0.01–0.88]	0.28 [0.01–1.14]	0.07	0.64
<i>Pinus coulteri</i>	0.13 [0.01–0.42]	0.11 [0.01–0.35]	–0.02	0.85
<i>Pinus muricata</i>	0.14 [0.00–0.57]	0.18 [0.01–0.70]	0.03	0.65
<i>Pinus sabiniana</i>	0.17 [0.01–0.66]	0.24 [0.01–1.01]	0.07	0.69
<i>Quercus douglasii</i>	0.28 [0.01–1.23]	0.30 [0.01–1.32]	0.02	0.69
<i>Quercus engelmannii</i>	0.21 [0.02–0.99]	0.32 [0.01–1.77]	0.11	0.62
<i>Quercus lobata</i>	0.29 [0.01–1.16]	0.28 [0.01–1.09]	–0.02	0.69
<i>Quercus wislizeni</i>	0.11 [0.00–0.40]	0.13 [0.01–0.50]	0.03	0.57
Averages	0.19	0.23	0.05	0.67

and period (Table 1). The spatial distribution of bioclimatic velocities for these California foothill and mountain pines and oaks exhibits high velocities leading to climatic unsuitability located in and around the large, flat Great Central Valley, whereas high velocities of increasing climatic suitability tend to concentrate in northern mountain ranges, although this pattern varied by species. Nevertheless, patterns of similarity emerge between species with overlapping ranges. For instance, *P. sabiniana* and *Q. douglasii* show a similar pattern of range dynamics and velocity; they increase at a higher rate in the northern mountains.

Predicted velocities are different for each period of analysis. Mean velocities suggest that most species analysed will experience higher bioclimatic velocities towards the end of the 21st century (LC), with an increase of  $0.05 \text{ km year}^{-1}$  on average with respect to the bioclimatic velocities of the MC

(Table 1). However, two species (*P. coulteri* and *Q. lobata*) show the opposite pattern (Table 1). Correlations between periods for each species are relatively high (0.67 on average, Table 1).

### The pace of climate change exposure for ranges

Species ranges (the extent of climatically suitable habitats) are predicted to shrink except for *P. balfouriana* in MC (Fig. 3a; SRC). Half of the species (4) have higher rates of loss in MC, and the other half in LC (Table 2). In general, differences in SRC between the two GCMs are larger for the MC projections than for the LC projections (Fig. 3a; Table 2; see also Appendix S3 in Supporting Information for range change maps by GCMs). REM is predicted to be higher in LC for the five of eight species analysed (Fig. 3b; Table 2). Likewise, the range of values of this metric

**Table 2** Comparison of metrics across species and projections

	Projection trends						Projection breadth trends						Variability	
	Increase			Decrease			Increase			Decrease				
	Small	Large	Total	Small	Large	Total	Small	Large	Total	Small	Large	Total	SD periods	SD species
SRC	3	1	4	4	0	4	1	0	1	7	0	7	0.22	0.50
REM	5	0	5	3	0	3	3	2	5	3	0	3	0.13	0.26
RCV	4	2	6	2	0	2	4	3	7	1	0	1	0.04	0.12
RSA	5	1	6	1	1	2	1	3	4	4	0	4	0.29	0.49
RSF	2	0	2	2	4	6	1	1	2	6	0	6	0.21	0.72
PCV	4	0	4	4	0	4	4	0	4	4	0	4	0.00	0.02
PCS	4	0	4	4	0	4	0	0	8	0	8	0.15	0.29	
PME	0	7	7	0	1	1	0	5	5	3	0	3	27.13	55.93
Average	3.375	1.375	4.75	2.5	0.75	3.25	1.75	1.75	3.5	4.5	0	4.5	3.5	7.3

Projection trends indicate the number of the eight species with a predicted increase or decrease for a metric between mid-21st-century projection [mid-century (MC)] and late-21st-century projection [late century (LC)]. Projection breadth trends indicate the number of species with an increase or decrease in the range of values from MC to LC according to the different global circulation models used. Large increases/decreases indicate that the magnitude of change in the metric is greater than the value of the metric in the MC, while small is less than that value. Variability indicates the standard deviation (SD) of the metric across species and periods. Metrics: species range change (SRC), range exposure to migration (REM), range change velocity (RCV), range spatial aggregation (RSA), range spatial fragmentation (RSF); population climatic velocity (PCV), population change in suitability (PCS) and population migration effort (PME). See Table S2 for individual metrics results.

increases in LC due to the differences in GCM projections (Table 2).

Bioclimatic velocity is generally higher in the leading edge than in the trailing edge (positive values in Fig. 3c), but the magnitude is species- and period-dependent (Fig. 3c). This pattern is reinforced in LC for six of eight species (Table 2), the exceptions being *Q. lobata* and *Q. wislizeni*. *P. muricata* and *P. coulteri* do not change notably between periods (Fig. 3c). The range of values of the metric (RCV) increases from MC to LC for seven of eight species (Table 2), and conflicting trends may appear under single GCM scenarios (see Appendix S4 in Supporting Information for GCM bioclimatic velocities). It is noteworthy that negative velocities are found within stable ranges (areas preserving climatic suitability), providing a signal of increasing exposure in such areas (see Fig. S2 in Supporting Information for velocities in stable ranges).

Landscape structure metrics (RSF and RSA) depict a general pattern (for five of eight of the species) of spatial erosion of the largest suitable patch combined with the loss of other small suitable patches (Fig. 3d,e). This pattern tends to be exacerbated in LC by decreased number of patches (three-quarters of the species) and increased aggregation (three-quarters of the species) (Table 2). There are exceptions to this pattern (*Q. engelmannii* and *P. sabiniana*) that also depend on the GCM projection (see bar ranges in Fig. 3d,e).

### The pace of climate change exposure for current woodlands

Woodlands are predicted to experience decreasing climatic suitability with climate change; the majority of plots experience negative bioclimatic velocities (PCV, Fig. 4a) and positive rates of suitability loss (PCS, Fig. 4b). However, a few

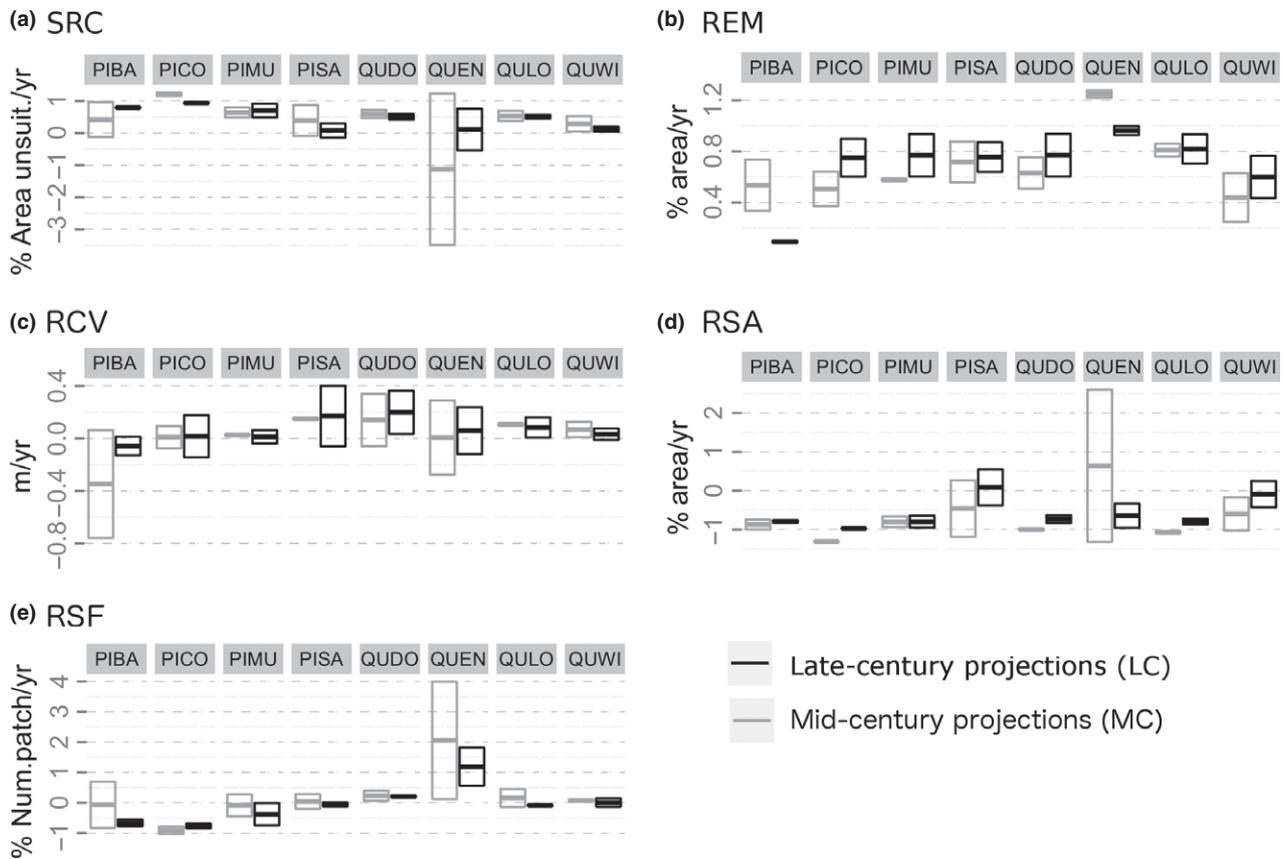
plots are projected to increase its climatic suitability (see bar depicting range of values). There is no general trend to whether these metrics increase (half of the species) or decrease (half of the species) depending on the temporal projection (MC or LC; Table 2).

The projected rate of isolation of current woodlands from potential suitable areas (measured by climate paths), or population migration exposure (PME, Fig. 4c), varies widely among species and time projections: from ca. 6 m year<sup>-1</sup> to 871 m year<sup>-1</sup>. For most species, this rate of climatic isolation doubles from MC to LC (seven of eight of the species; Table 2). The presence of many outliers indicates disjunct populations (Fig. 3c). This is especially the case for *P. balfouriana* with a few southern populations predicted to become very isolated in LC (Fig. 4c).

### Varying exposure rates

The rates of exposure (averaging across metrics) increase towards the LC for 4.75 of 8 species on average (Table 2), and the uncertainty in the metrics derived from using different GCMs decreases towards LC for 4.5 of 8 species on average (Table 2). Exposure rates are more sensitive to species than temporal projections, with average standard deviations of the metrics among species (7.3) being greater than across periods (3.5), and this pattern remains constant for all metrics analysed (Table 2).

Three species (*P. balfouriana*, *P. muricata* and *Q. wislizeni*) depict very similar exposure rates between periods for all metrics, while exposure rate is dramatically increased or decreased in one or more dimensions for other species (e.g. *Q. engelmannii*, *P. coulteri*; Fig. 5a). Similarities between species and periods suggest processes (e.g. dispersal, migration)



**Figure 3** The pace of climate change exposure in range-level metrics. Mid-century projections are in light grey, and late-21st-century projections in black. Hollow bars indicate the range of the two global circulation models (GCMs) predictions, and middle bar indicates average. (a) Species range change (SRC); (b) range exposure to movement (REM): time rates between full versus null dispersal in their ranges; (c) range change velocity (RCV): differences between velocities of leading edge and trailing edge; (d) range spatial aggregation (RSA): percentage of area change of the species' largest suitable habitat patch per unit of time; (e) range spatial fragmentation (RSF): percentage of patch abundance increase/decrease per unit of time. Species abbreviations are defined in Fig. 2 caption. See Table S2 (Supporting Information) for individual metrics results.

that may play key roles in exposure for each time frame analysed (Fig. 5b).

## DISCUSSION

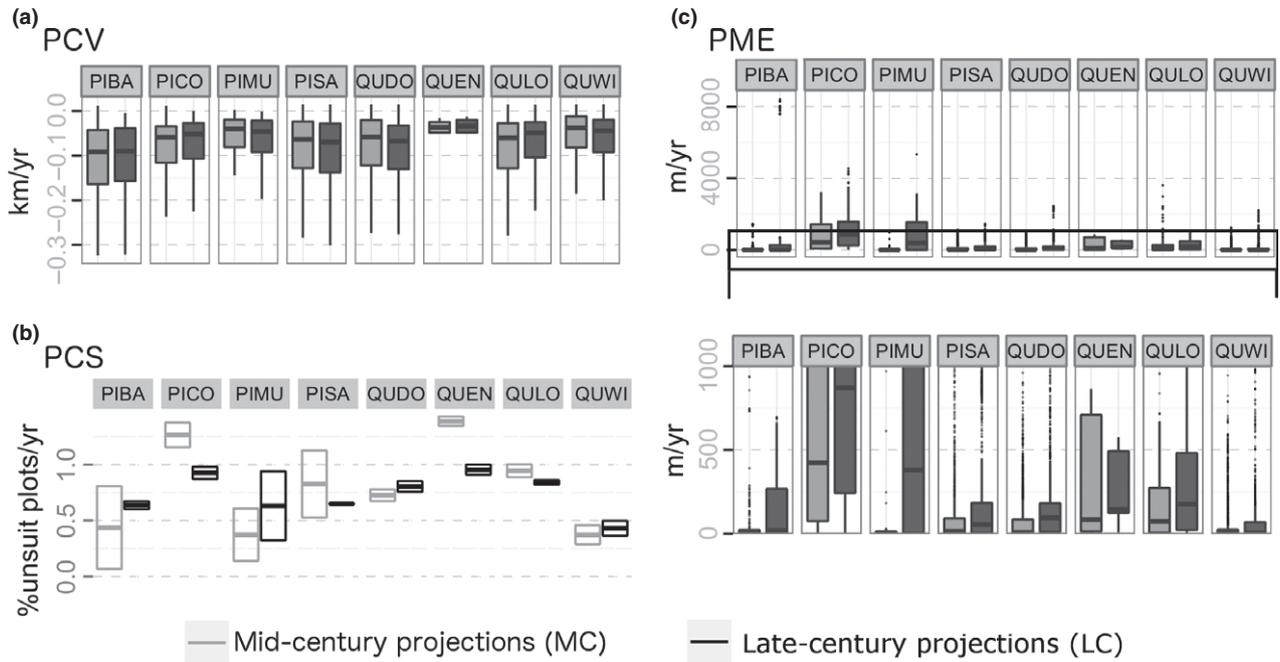
### Measuring the pace of changing climatically suitable conditions: bioclimatic velocity

The bioclimatic velocity measurement proposed in this study extends the concept of climate velocity to depict species-specific exposure to climate change. That translation from physical attributes (e.g. temperature, precipitation) to an integrated measurement of climatic suitability has the advantage of depicting how fast suitable conditions appear or disappear for a given species and period.

The bioclimatic velocity maps show congruent patterns using analogous metrics to climate velocities presented in Loarie *et al.* (2009), Ackerly *et al.* (2010) and Dobrowski *et al.* (2013) for temperature, precipitation and actual evapotranspiration in California. Flat areas exhibit higher velocities than mountainous areas where varying climatic conditions in

space tend to be large. This steep spatial gradient thus reduces velocity estimates in mountainous areas.

Bioclimatic velocities are slightly lower than the climate velocity presented for a larger extent by Ackerly *et al.* (2010): 0.21 km year<sup>-1</sup> for bioclimatic velocity (average of species and periods) compared to 0.24 km year<sup>-1</sup> for mean temperature velocity. Also, the range of our 5–95 percentiles is generally lower than those in Ackerly *et al.* (2010): they estimated 0.03–4.89 km year<sup>-1</sup> for temperature velocity and 0.01–0.92 km year<sup>-1</sup> for precipitation velocity in the drier scenario (GFDL) and 0.01–0.46 km year<sup>-1</sup> for precipitation velocity in the wetter scenario (PCM), whereas bioclimatic velocity in our study ranged from 0.01 to 0.89 km year<sup>-1</sup>. Some discrepancies would be expected because the use of SDMs to transform combinations of raw climate variables into an associated measure of habitat suitability may affect the spatial variation of suitability relative to that of climate alone. Ultimately, the spatial gradient affects the magnitude of the velocity being estimated. Therefore, it is not surprising that bioclimatic velocities could be different than climate velocities. In our study, we used an ensemble of SDMs to



**Figure 4** The pace of climate change exposure in plot-level metrics (current distribution). Mid-century projections are in light grey, and late-21st-century projections in black. Hollow bars indicate the range of the two global circulation models (GCMs) predictions, and middle bar indicates average. Boxplots indicate the distribution of values in current plots. (a) population change in bioclimatic velocity (PCV): velocity of bioclimatic exposure in species plots; (b) population change in suitability (PCS): percentage of plots becoming unsuitable per unit of time; (c) population migration exposure (PME): cost-distance to the nearest suitable patch. Inset represents zoom to the interquartile distribution of values. Species abbreviations are defined in Fig. 2 caption. See Table S2 for individual metrics results.

address the inherent uncertainty of using different statistical approaches (Araújo & New, 2007). However, further research on bioclimatic velocity could estimate the sensitivity of bioclimatic velocity to the SDM technique used.

Spatial resolution is another source of variation between climate and bioclimatic velocity estimates. Dobrowski *et al.* (2013) found that coarser resolutions increase estimates of climate velocity, and therefore, it is not surprising that bioclimatic velocities presented here and based on 270-m resolution data are lower than climate velocities found by other authors who used coarser climate grids (e.g. Loarie *et al.*, 2009; Burrows *et al.*, 2011; Dobrowski *et al.*, 2013).

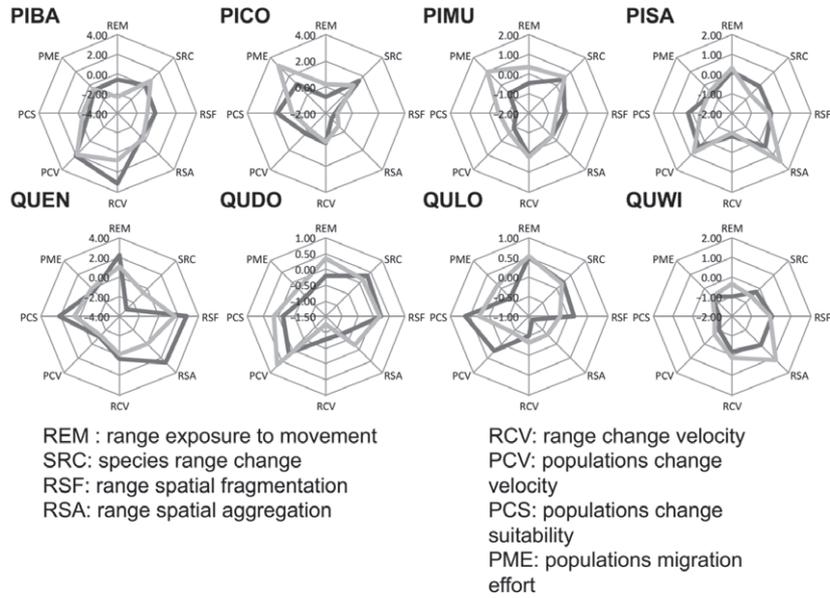
### Individualistic paces of exposure to climate change

We illustrate that the velocity of species' exposure to climate change varies depending on the species, within each species range and period under analysis. These results reinforce the importance of transforming from physical climate space to biotic climate space (suitability), as differences are clear even in the case of similarly distributed species and using the same predictor variables. Broadly, the results presented in this study are generally consistent with other projections of range shrinkage, fragmentation and overall loss of climatic suitability for plant species in the study region (Loarie *et al.*, 2008; Franklin *et al.*, 2013), but here we illustrate the inherent variation in the rates of change of metrics that are indices of exposure risk and potential woodland dynamics.

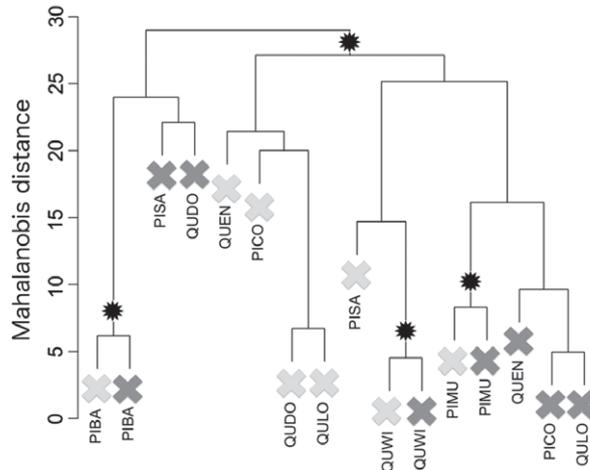
The taxonomic and temporal variation found in this study largely supports the conclusions raised by several modelling and observational studies, which have also identified diverse patterns of range dynamics at the specific level. For instance, in our case, the velocity of gaining environmental suitability in potential leading edges of ranges is generally higher than the suitability loss in trailing edges. Accordingly, some studies have shown that the leading edge of the range may become occupied at higher rates than the trailing edge is vacated (Chen *et al.*, 2011 showed for Lepidoptera). However, other studies have suggested that most tree species may not be able to keep pace with expansion of suitable habitat at the leading edge (Foden *et al.*, 2007; Murphy *et al.*, 2010), although such response may be species specific (Zhu *et al.*, 2012). In these cases, accumulation of extinction debt may occur at trailing edges especially for long-lived organism such as trees (Kuussaari *et al.*, 2009). These effects could ultimately result in shrinking distributions. Our study emphasizes a common trend of range reduction (range metrics: SRC, RSF, RSA) and an overall increased exposure of populations (plot metrics: PCS, PCV), although at different paces depending on the species and differentially across populations.

All in all, temporal variations in exposure generally support the idea of an acceleration of exposure by the end of the century, coinciding with major predicted changes in temperature and precipitation (Cayan *et al.*, 2009). However, this support is not strong (five of the eight species showed

(a)  
Extent of species-period exposure



(b)  
Similarity between species-period exposure



**Figure 5** Differences in the pace of climate change exposure among species and periods across all metrics: (a) extent of exposure rates across species for mid-21st-century projections [mid-century (MC), grey], late-21st-century projections [late century (LC) dark grey] and (b) dendrogram of similarity among species-projection rates. Dark grey cross and light grey cross indicate LC and MC, respectively. Black stars in the dendrogram indicate high similarity among the two time periods: the majority of species below the branch contain both LC and MC projections of the same species. Species abbreviations are defined in Fig. 2 caption.

increasing bioclimatic velocity estimates) and especially low in the case of current population-level metrics (PCV, PCS). These results emphasize that adaptive capacity may be crucial for some species, as changing suitability will challenge some species faster than others and may occur sooner than later.

**Challenges ahead: climate variability, extremes and microclimates**

The metrics used in this study constitute a first approximation of the velocity of species exposure of climate change. However, it is noteworthy that the application of SDMs to assess exposure in dynamic environments may be further limited by the static nature of the models and the scale of analysis (Franklin, 2010b), in addition to other widely discussed limitations (see Fitzpatrick & Hargrove, 2009; Franklin, 2010a; Keenan *et al.*, 2011; Schwartz, 2012).

In previous studies of the velocity of climate change, temporal gradients were estimated with a linear regression over time. Therefore, climate variability and extremes are indirectly taken into account. For instance, Dobrowski *et al.* (2013) used a yearly interpolation of climate variables to calculate velocity of climate, which further provided a measure of significance for velocity, after correcting for temporal auto-correlation. In contrast, SDMs with their quasi-equilibrium assumption and reliance on species distribution data for adult or mixed-age individuals are usually calibrated from and projected to climatic scenarios (30-year averages define climate); therefore, these models are not suitable for providing velocity estimates at finer temporal resolutions.

In our case, an SDM implementation using climate variables at finer temporal resolution would face several challenges. First, the role of climate variability and extremes in shaping plant species distribution is poorly understood. On

the one hand, extreme events are shown to increase model accuracy (albeit weakly) for species distributions (Zimmermann *et al.*, 2009), but Larcher & Mair (1969) showed that temperature extremes alone could not explain range limits in Mediterranean oaks. Altogether, it may be difficult to disentangle both roles using correlative approaches, as means and extremes tend to be highly correlated.

Second, weather variability differentially affects tree life stages, which may confound the response variable of SDMs. That is, seedling survival and germination may be strongly affected by this variability (Thompson *et al.*, 2012; Nabel *et al.*, 2013), but advanced life stages of trees may not. Crucially, this issue affects range migration estimates (Early & Sax, 2011; Bennie *et al.*, 2013), but may not be meaningful for plot-level metrics of suitability (e.g. conditions of the current distribution of adult trees) as adults are far more resilient (Lloret *et al.*, 2012). Interestingly, SDMs can be fit using weather variables together with climate means for vagile organisms (see Reside *et al.*, 2010; Bateman *et al.*, 2012; and VanDerWal *et al.*, 2013). Indeed, such an approach is appropriate for mobile organisms or those with a short life cycle because their distribution is able to reflect variation in climate at finer temporal resolution. Third, it may be contentious to use GCM projections of climate variability and extremes (in contrast to observations of historical variability) to provide a framework for evaluating significant trends. Unlike averaged values, finer temporal and spatial resolutions and extreme events still report considerable uncertainty, even with the recent advancements of new generation of GCM (Sillmann *et al.*, 2013).

The role of microclimates (and thus spatial resolution of the analysis) can be very important in buffering future temperature and precipitation changes (Bennie *et al.*, 2013; Lenoir *et al.*, 2013). Exposure estimates should reflect such variations in space. In our study region, analogous spatial resolution sensitivity analysis has also been performed for SDMs. Franklin *et al.* (2013) showed that there are large differences (both omission and commission) between suitable habitats predicted from coarse- versus fine-scale climate grids, concluding that the 270-m resolution used in the present study is adequate to capture some fine-scale effects of topoclimate on species distributions.

## CONCLUSIONS

Transformation of physical climate space to a more biologically meaningful climate space can support species-specific conservation measures. Our results emphasize that climate velocities can be species specific but may vary within its range and among periods. Areas of low bioclimatic velocity may be high-priority targets for *in situ* conservation (land conservation, woodland reserves) for a given species and time period, while areas of high velocity increases in habitat suitability may be appropriate targets for, for example, climate change adaptation strategies such as managed relocation. Areas of rapidly decreasing suitability, especially for

species whose plot metrics also suggest increasing exposure, would indicate to managers where woodland health may be expected to decline and where community changes may be anticipated. Limitations still constrain the use of SDMs to make dynamic predictions, however, and careful calibration and sufficient ecological data are necessary for meaningful habitat suitability estimates.

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## SUPPORTING INFORMATION

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

**Appendix S1** Species distribution models outline.

**Appendix S2** Metrics of exposure descriptions.

**Appendix S3** Range Change maps for each species, GCM and period.

**Appendix S4** Bioclimatic velocity maps for each species, GCM and period.

**Figure S1** Boxplots of accuracy results.

**Figure S2** Boxplot of averaged bioclimatic velocity in ranges.

**Table S1** Accuracy results of species distribution models.

**Table S2** Results of metrics of exposure.

## BIOSKETCH

**Josep M. Serra-Diaz** is interested in combining different approaches to model global change impacts across taxa and ecosystems at different temporal and spatial scales.

Author contributions: J.M.S.D. and J.F. designed the research with input from all authors; A.D.S., F.W.D. and M.I. provided data; J.M.S.D. performed the modelling; J.M.S.D. and J.F. wrote the first draft of the manuscript; and all authors participated in writing subsequent drafts.

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