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ORIGINAL ARTICLE

Hotspots and ecoregion vulnerability driven by climate change velocity in Southern South America

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Abstract

Any conservation strategy must deal with the uncertainty caused by anthropogenic climate change. In order to forecast such changes, the climate change velocity approach has been used to measure ecosystem exposure to this phenomenon. The Tropical Andes and the Chilean Winter Rainfall-Valdivian Forests (Central Chile) hotspots are priority for conservation due to their high species richness and threats, where climate change is one of the serious pressures to their ecosystems. Even though previous studies have forecasted future climate velocity patterns across the globe, these biodiversity hotspots lack a regional evaluation of the vulnerability to climate change to inform conservation decisions. In this study, we evaluated the vulnerability of terrestrial ecosystems to climate change velocity at the Southern South America ecoregional system, by using regional climatic data that improves the accuracy of predictions. We estimated forward and backward velocities for temperature and precipitation, and we performed a protected area-level analysis of climate change vulnerability. Also, we compared our results with previous evaluations. We found that forward velocity was higher in the Tropical Andes hotspot for both climatic variables analyzed, whereas backward velocity was higher in the Central Chile hotspot considering just the temperature variable. Finally, we found that in the Central Chile hotspot, smaller protected areas are more vulnerable to climate change as measured by climate change velocity, whereas in the Tropical Andes hotspot, larger protected areas are more vulnerable. Several rapid change areas are expected along the two hotspots. These findings have important conservation implications in the region, especially for the protected areas.

Keywords Climate change velocity · Tropical Andes · Central Chile · Ecosystem vulnerability · Biodiversity hotspots

Introduction

Anthropogenic climate change is one of the key pressures to biological, physical, social, and economic systems (IPCC 2014, 2018). Biotic and abiotic responses associated with changes in new climate conditions have been widely documented during the last century (Parmesan and Yohe 2003; Dawson et al. 2011; Fei et al. 2017). Moreover, climate change will experience rapid rates of change towards novel climatic conditions and will cause the disappearance of some extant climates (Williams et al. 2007).

There is no guarantee that ecosystems will be able to circumvent such changes at accelerated rates; in fact, ecosystems worldwide are collapsing as a result of climate- and human-induced changes (Bland et al. 2017). Ecosystem collapse may involve biodiversity loss, which has been reported as one of the most serious menaces to ecosystems, threatening ecosystem functions and services, as well as threatening human welfare (Millennium Ecosystem Assessment 2005; Cardinale et al. 2012; Steffen et al. 2015). Furthermore, the uncertainty caused by climate change (Yousefpour and Hanewinkel 2016) and our limited capacity to understand the risks and forecast ecosystem collapse (Bland et al. 2017) are the main challenges for conservation strategies that support adaptation to global environmental change (Pressey et al. 2007; Lawler et al. 2015).

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Ecosystem exposure to climate change corresponds to the degree in which an ecosystem is exposed to climate variations over time or space (Garcia et al. 2014). To assess such exposure, it is important to know how fast the climate is shifting, as well as the direction of that change (Loarie et al. 2009; Dobrowski et al. 2013; Nadeau et al. 2017). Climate change velocity (Loarie et al. 2009; Hamann et al. 2015) is a regional-type metric and one of the most widely used for estimating climate change exposure (Garcia et al. 2014), which represents the rate and direction at which organisms or ecosystems require to migrate while maintaining constant climatic conditions (Loarie et al. 2009; Dobrowski et al. 2013). Moreover, climate change direction provides information about how climate shifts will vary across the landscape (Garcia et al. 2014), reflecting topographic aspects, or regional climate change (Ackerly et al. 2010).

Climate velocity can be estimated using several methodologies (Garcia et al. 2014; Brito-Morales et al. 2018), but two main approaches have been used to calculate it, namely local velocity (Loarie et al. 2009) and analogue-based velocity (Ordonez and Williams 2013; Hamann et al. 2015). The former considers the climate spatial variation within the neighborhood of a specified location (Loarie et al. 2009; Carroll et al. 2015). The second approach (analogue-based velocity) represents the actual distance to where the nearest analogous climates will be found in the future. It can describe the speed and direction of climate variation based on landscape heterogeneity and is facilitated by efficient nearest-neighbor search algorithms (Hamann et al. 2015). Climate change velocity applications have focused on assessing the following: (1) climate vulnerability of conservation areas (Loarie et al. 2009; Ackerly et al. 2010; Schueler et al. 2014; García Molinos et al. 2017); (2) climate change exposure of marine and terrestrial environments (Burrows et al. 2011, 2014; Diffenbaugh and Field 2013); and (3) species vulnerability, migration capacity, or refugia (Schippers et al. 2011; Sandel et al. 2011; Bateman et al. 2012; Schueler et al. 2014; Serra-Diaz et al. 2014; Hamann et al. 2015; Roberts and Hamann 2016; García Molinos et al. 2016; Carroll et al. 2017; Williams and Blois 2018).

Terrestrial ecosystems have experienced widespread changes due to climate over the last century that span the biological hierarchy from genes to communities and are expected to intensify in the next few decades (Scheffers et al. 2016). This rate of change is expected to be at least an order of magnitude, if not several orders of magnitude faster, than the changes to which terrestrial ecosystems have been exposed to during the past 65 million years (Diffenbaugh and Field 2013).

Global and continental climate velocity estimations have indicated that mountain regions with high spatial climate heterogeneity will exhibit slower velocity rates, while flatter topographical regions will exhibit faster velocities (Loarie et al. 2009; Carroll et al. 2015). This aspect has been analyzed by Dobrowski and Parks (2016), who remarked how mountain climate velocity had previously been underestimated, showing that distance is not the best metric to measure climate connectivity in these zones; and suggesting climate velocity can be higher in mountains as they are more isolated and provide climatic resistance to species movement. However, it is still uncertain how climate velocity will be able to determine conservation plans in complex terrestrial ecosystems such as mountains.

Southern South America (SSA) includes four of the world's five major climate zones (Tropical, Mediterranean, Temperate, and Boreal) and harbors 2 out of 35 of the world's biodiversity hotspots: Tropical Andes and Winter Rainfall-Valdivian Forests (ChV) in Central Chile. These areas exhibit great species (Tropical Andes) and genus (ChV) richness of vascular plant species and high endemism of animal species; both are already experiencing a high degree of habitat loss (Myers et al. 2000; Mittermeier et al. 2004, 2011).

Even though previous studies have forecasted future climate velocity patterns across the globe including SSA (e.g., global analysis by Loarie et al. 2009; Burrows et al. 2011, 2014; and a continental analysis by Carroll et al. 2015), biodiversity hotspots in SSA lack a regional evaluation of climate velocity to determine the vulnerability to climate change that may lead to different conclusions regarding conservation actions.

This study set out to quantify the vulnerability of terrestrial ecosystems to climate change in the SSA ecoregional system. We focused on answering two main questions: (1) How will the magnitude and rate of climate change velocity be projected in SSA hotspots and ecoregion units? (2) Which ecoregion units in SSA will be more vulnerable to climate change, as measured by climate change velocity?

To address these questions, we assessed an ecoregional vulnerability in SSA using a forward and backward velocity approach (Carroll et al. 2015) and estimated the climate change direction for the two biodiversity hotspots and ecoregions recognized in this area. Also, we compared our results with previous evaluations. The forward and backward climate change direction for each ecoregion and hotspot has not previously been evaluated for SSA.

Methods

Study area and ecoregion units

We considered the SSA section to include Chile (Fig. 1a), southern Perú, southwestern Bolivia, and north western Argentina. To define terrestrial ecosystem units at a broad level, we used an ecoregional classification following Dinerstein et al. (2017). This area includes 16 ecoregions:

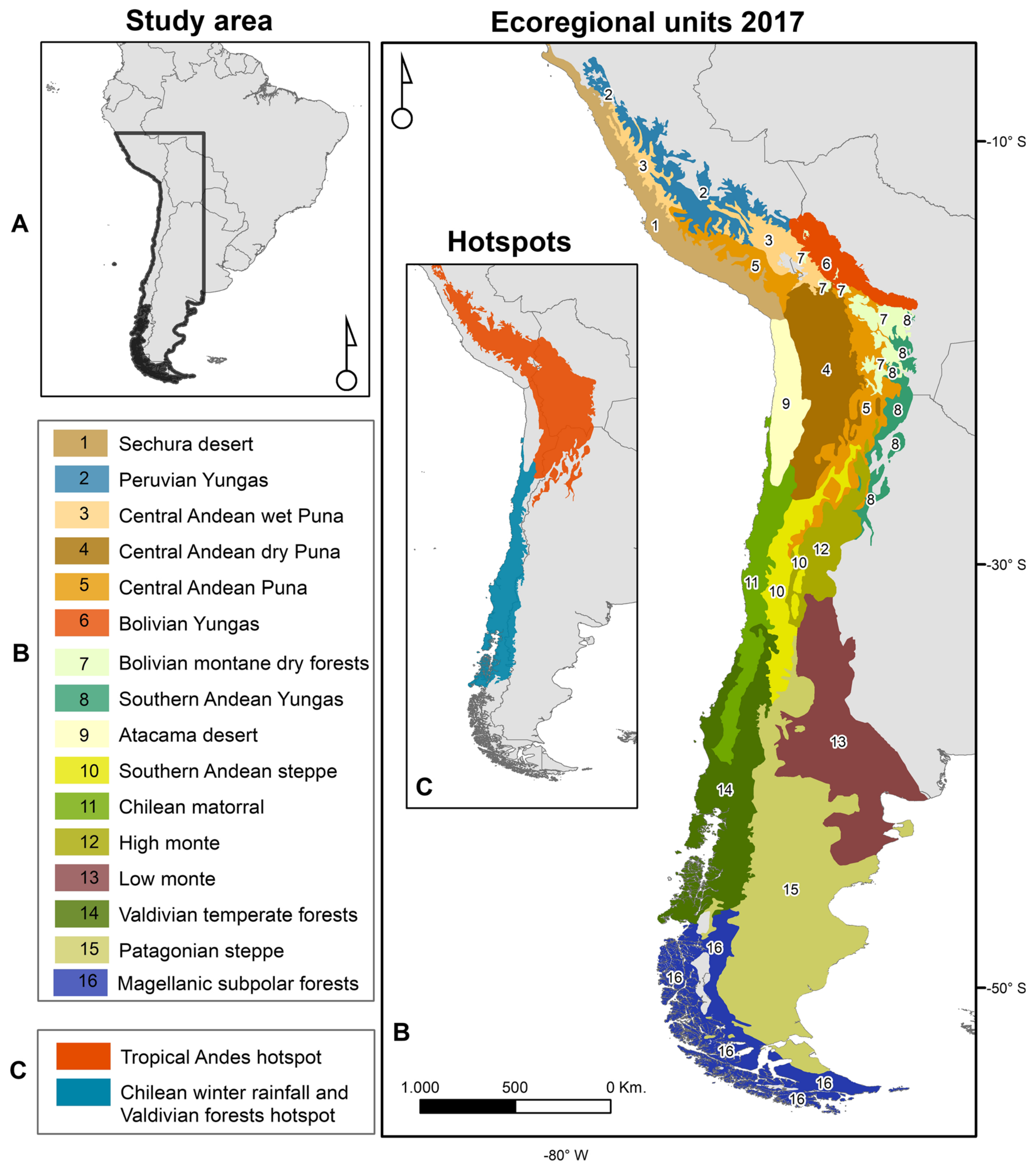

Fig. 1 Hotspots and ecoregions in Southern South America (SSA). The upper left figure depicts the study area (**a**), the right figure shows the world ecoregions considered (**b**), and finally, in the middle panel (**c**), the two hotspots of SSA evaluated in this study

the Sechura Desert, Peruvian Yungas, Central Andean Puna (wet and dry), Bolivian Yungas, Bolivian montane dry forests, Southern Andean Yungas, Atacama Desert, Southern Andean Steppe, Chilean Matorral, High Monte, Low Monte, Valdivian Temperate Forests, Patagonian Steppe, and Magellanic Subpolar Forests (Fig. 1b). In the case of Peruvian Yungas, we considered the ecoregion limits suggested by Olson et al. (2001) and revalidated by Britto (2017). SSA presents different topographical attributes, mostly arising from the Andes mountain range across the study area. Three climatic domains can be found across the study area: Tropical, Mediterranean, and Temperate. Ecoregions which present a Tropical climate-type can be found in Perú, Bolivia, and northern Chile. Mediterranean climate-type can only be identified in central Chile, whereas Temperate climate-type can be found in southern regions of Chile and Argentina. Mountainous topography can be identified along most of the 16 ecoregions, with some exceptions where flat areas can be found, at either high or low altitude. These exceptions include ecoregions located in the high Andes (Puna) which corresponds to a flat plateau (3, 4, and 5 in Fig. 1), those located in the coastal area towards the Pacific Ocean in Perú and Chile (1, 9, and 11 in Fig. 1), and those present in the western slope of the Andes in Argentina, dominated by a flat terrain (13 and 15 in Fig.1).

Present and future climate data

Current bioclimatic surfaces in SSA were obtained from Pliscoff et al. (2014), which considered a spatial resolution of 1 × 1 km, representing a time period of 50 years (1950–2000), and a dense dataset of meteorological stations—930 meteorological stations located in Chile, Bolivia, Perú, and Argentina—resulting in a more accurate database than previously available (e.g., Worldclim, Hijmans et al. 2005). This climatic baseline has been used by subsequent studies for it being a better fit for SSA (Valenzuela-Sánchez et al. 2014; De Porras et al. 2015; Larridon et al. 2015; Martinez-Harms et al. 2017; Espíndola and Pliscoff 2018).

We incorporated this baseline to infer future climate predictions for annual mean temperature and annual precipitation, using the delta statistical downscaling method (Hijmans et al. 2005; Ramírez-Villegas and Jarvis 2010). Climatic anomalies represent the comparative difference between future and present climate (deltas). Anomalies of original global circulation models (GCM) were obtained and then applied to the baseline climatic data. GCM deltas were sourced from the Global Climate Model data portal (Ramirez-Villegas and Jarvis 2008) (http://www.ccafs-climate.org) for periods 2030 (average for 2021–2040) and 2080 (average for 2071–2090) for two IPCC Representative Concentration Pathways (RCP): RCP2.6 and RCP8.5. The RCPs are identified by their approximate total radiative forcing in the year 2100 relative to 1750: 2.6 W per square meter (W/m^2) for RCP2.6 and 8.5 W/m^2 for RCP8.5 (IPCC 2014). RCP2.6 represents a scenario where radiative forcing peaks at approximately 3 W/m^2 before 2100 and then declines (van Vuuren et al. 2011; IPCC 2014). RCP8.5 represents a scenario characterized by an increasing greenhouse gas emission trajectory over time, with radiative forcing consequently increasing to 8.5 W/m^2 in 2100 (Riahi et al. 2011; IPCC 2014).

Emission scenarios were used for the CMIP5 multi-model dataset by 31 GCMs in the RCP8.5 scenario and 25 GCMs were used for the RCP2.6 scenario based on their availability in the Global Climate Model data portal. The total GCMs utilized were as follows: CSIRO-ACCESS1.0, CSIRO-ACCESS1.3, BCC-CSM1.1, BCC-CSM1.1(m), BNU-ESM, CanESM2, CCSM4, CESM1(BGC), CESM1(CAM5), CSIRO-Mk3.6.0, EC-EARTH, FIO-ESM, GFDL-CM3, GFDL-ESM2G, GFDL-ESM2M, GISS-E2-H, GISS-E2-R, IPSL-CM5A-MR, INM-CM4, IPSL-CM5A-LR, FGOALS-g2., MIROC-ESM, MIROC-ESM-CHEM, MIROC5, HadGEM2-CC, HadGEM2-ES, HadGEM2-AO, MPI-ESM-MR, IPSL-CM5B-LR, MRI-CGCM3, and NorESM1-M.

Climate change velocity algorithm

We used the analogue-based velocity approach (Hamann et al. 2015) to estimate the forward and backward velocity and direction of temperatures and precipitation variables, according to each GCM. *Forward velocity* describes the distance from current climate locations to their nearest analogous sites in the future. In contrast, *backward velocity* describes the distance from future projected climatic cells back to current analogous climate locations (Carroll et al. 2015). Forward and backward climate analogues were identified using a univariate k-nearest neighbor search algorithm between present and future data (Appendix S6 in Hamann et al. 2015), where analogue distances were measured as Euclidean. Furthermore, to obtain forward and backward climate directions, we computed the azimuth angles between the closest analogue climate match vectors, given the result of the univariate k-nearest neighbor search algorithm. Angles were calculated in degrees among each coordinate data pair.

Moreover, to deal with GCM variation, we calculated the total climate velocity average from all GCMs, at each RCP scenario and period (2030 and 2080). Climate change velocity uncertainty was estimated by the standard deviation of velocities across the multiple GCMs, where lower and upper uncertainty were defined by RCP2.6 and RCP8.5 scenarios, respectively, following the approach by Loarie et al. (2009).

All of these estimations were computed using the R-Project software version 3.5.1 (R Development Core Team 2018). All computational calculations were done at the supercomputing infrastructure of the National Laboratory for High-Performance Computing in Chile (NLHPC) (ECM-02).

To evaluate our regional results regarding previous climate change velocity estimations on a continental scale, we compared our results with Carroll's velocity calculations for SSA, whose data is available at https://adaptwest.databasin.org. Specifically, we contrasted the forward and backward velocity averages of temperatures at each hotspot and their spatial patterns. Then, we compared two GCMs: HadCM3 (CMIP3)—used by Carroll et al. (2015)—and HadGEM2-ES (CMIP5)—used in this study—where we considered a 50 × 50-km pixel size for both data sources.

Hotspot vulnerability to climate change velocity

We analyzed the vulnerability of two major hotspots in SSA, the Tropical Andes and the Chilean Winter Rainfall-Valdivian Forest hotspots (ChV) (Myers et al. 2000; Mittermeier et al. 2011). The Tropical Andes hotspot in SSA includes the following ecoregions: the Peruvian Yungas, the Central Andean Puna (wet and dry), the Bolivian Yungas, the Bolivian montane dry forests, and the Southern Andean Yungas, whereas the ChV hotspot includes the Chilean Matorral and the Valdivian temperate forest (Fig. 1c).

The vulnerability assessment approach follows the forward-backward velocity assessment described by Carroll et al. (2015), where the linear relationship between forward (x-axis) and backward (y-axis) velocity suggests four threat quadrants, which are defined by the median of each metric. The interpretation of this relation is described as follows: high rates of forward-velocity (km/year) suggest threats to local populations, whereas high rates of backward-velocity suggest threats to sites. Likewise, a higher forward-backward relationship velocity suggests simultaneous threats to sites and populations. Finally, a slower forward-backward relationship implies a low threat.

Forward and backward velocity averages for each ecoregion and hotspot were calculated for each scenario and for climate variable considered. In addition, we also evaluated the relation between the size of Protected Areas and the climate change velocity metric at each hotspot. Protected Areas were sourced from the World Database on Protected Areas (UNEP-WCMC, IUCN 2018). See Methods overview in Fig. 2.

Results

Climate change velocity behavior in Southern South America hotspots and ecoregions

Velocity of climate change

Our results suggest that forward velocity was much higher in the Tropical Andes hotspot than in the ChV hotspot, for both climatic variables (temperature and precipitation) (see Fig. 3, Fig. S1 and Fig. S2 in the Online Supplement). Conversely, backward velocity was higher in the ChV hotspot, but only for the temperature variable. The differences between hotspots are seen more clearly for the RCP8.5-2080 scenario when considering temperature velocity (Fig. 3), as follows: Tropical Andes hotspot forward (0.48 km/year, mean; 0.29 km/year, median) and backward velocity (0.71 km/year, mean; 0.37 km/year, media); and a ChV hotspot forward (0.27 km/year, mean; 0.19 km/year, median) and backward velocity (1.81 km/year, mean; 1.44 km/year, median).

At the ecoregional scale, higher backward rates were concentrated in central Chile and southern ecoregions (Chilean Matorral, Valdivian, and Magellanic forests), and were also over 1 km/year in the Atacama Desert in the case of temperatures when considering the RCP8.5 scenario. Results show a north-south trend in velocity, being higher in ecoregions of northern Chile, northern Argentina, Southern Perú, and Southwest Bolivia (Central Andean Puna, wet and dry). Mean value rates can be found in coastal ecoregions of north-Chile and Perú (Sechura and Atacama deserts), and lower rates were seen in all ecoregions of central and Southern Chile and Argentina, with the exception of Low Monte and the Patagonian steppe ecoregions. The forward and backward velocities for each ecoregion are reported in Table 1 for temperatures and in Table S1 for precipitation (see Online Supplement).

Uncertain spatial patterns of temperature velocity were spatially confirmed beyond the ecoregional area analyzed for both forward and backward surfaces (see Fig. S8 in the Online Supplement). In the case of precipitation, uncertainty was higher in the Patagonian steppe ecoregion, outside the two analyzed hotspots. Future precipitation patterns in climate change scenarios have been reported with major uncertainty levels for the South American Altiplano (Minvielle and Garreaud 2011). We also found major uncertainty in the spatial patterns for precipitation in the Central Andean wet Puna ecoregion for RCP8.5-2030 period (see Fig. S9 in the Online Supplement).

Direction of climate change

The Tropical Andes hotspot exhibited a direction of change towards southern latitudes based on temperature and precipitation in the most conservative scenario (RCP2.6). In contrast, the ChV hotspot exhibited different trajectories for temperature, particularly in the RCP8.5-2080 scenario, showing both forward (northwest and southwest) and backward estimations (northeast and southeast) (Fig. 3). As part of the ChV hotspot, the Chilean Matorral exhibited the most north-westerly direction for temperature in all scenarios (Fig. S3 in the Online Supplement), which points at the influence of tropical climate in this ecoregion, in contrast to the Chilean Mediterranean macrobioclimate (Luebert and Pliscoff 2017).

The Atacama and Sechura Deserts presented a predominantly north-westerly direction of change considering temperature (Fig. S3 in the Online Supplement), and a south-westerly direction for precipitation change (Fig. S4 in the Online Supplement). These desert environments are defined by flat coastal areas and low mountain ranges, where the Atacama Desert has the flattest topography of the two. In the case of the Peruvian and Bolivian Yungas, temperatures shifted towards the northwest and northeast (Fig. S3 in the Online Supplement), and these patterns changed to the southwest in the backward velocity scenario (Fig. S4 in the Online Supplement). The topography of the Yungas is characterized by an abrupt mountain range. The Central Andean Puna and its divisions—dry and wet Puna—also showed temperature movement to the south and southwest. These ecosystems are characterized as highland plateaus. However, the RCP8.5-2080 scenario featured climate velocity directions that varied from the other scenarios: the temperature moved southwest for the Central Andean Puna, west for the dry Puna, and northwest for the wet Puna

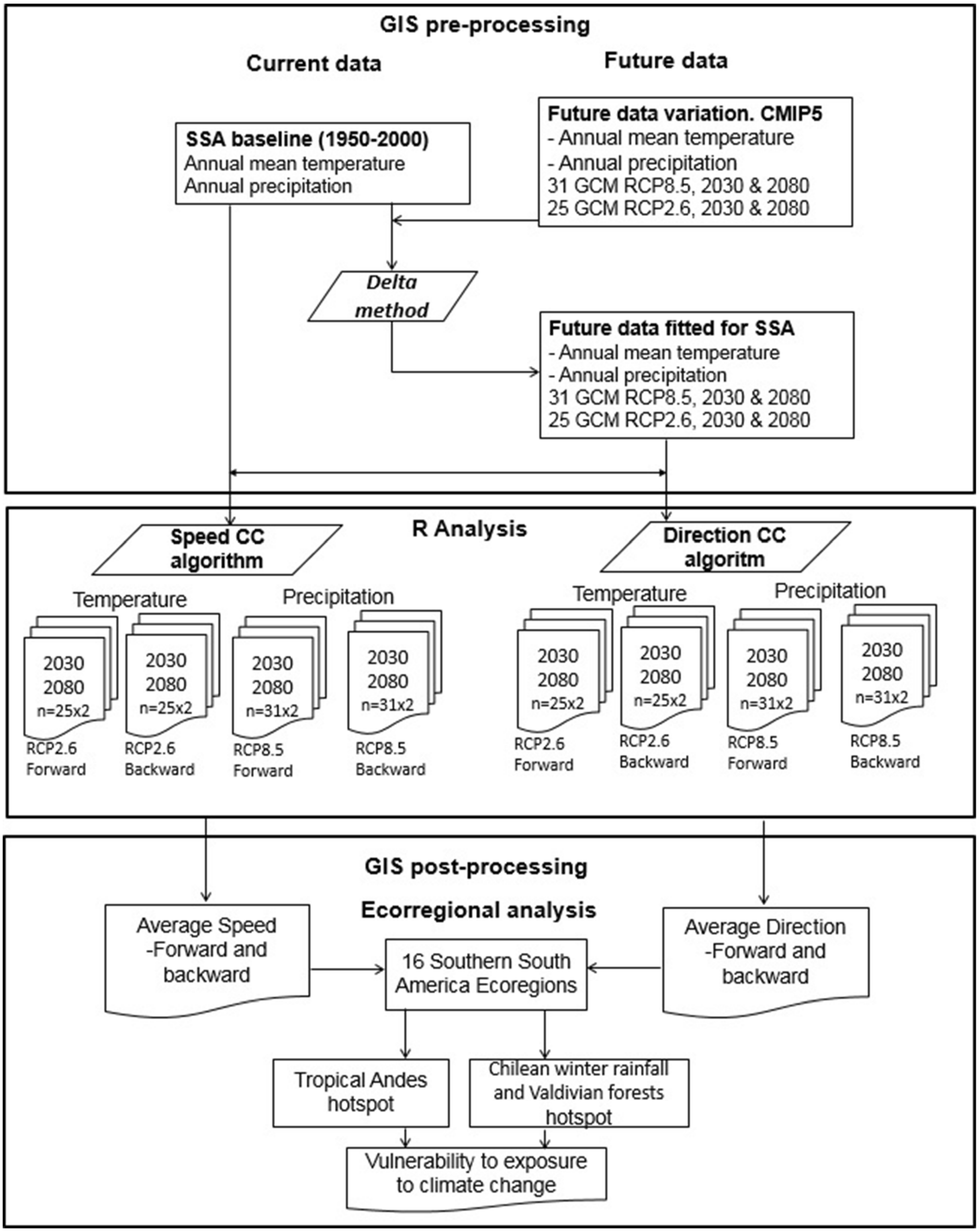

Fig. 2 The methodological developed process. Including (A) GIS pre-processing, (B) analysis in the R environment, and (C) GIS post-processing steps. The abbreviations used in the scheme are described below: geographic information system (GIS), Southern South America (SSA), global circulation model (GCM), and climate change (CC)

(Fig. S3 in the Online Supplement). Finally, the Patagonian steppe and Magellanic forest exhibited predominant directions towards the southeast. Steppe ecosystems show one of the flattest topographies of SSA; meanwhile, the Magellanic forest has a mountainous topography (Fig. S3 in the Online Supplement).

Previous climate change velocity evaluations in Southern South America

Our regional results compared with Carroll's velocity calculations for SSA (Carroll et al. 2015) featured spatial differences for temperature velocity (see Fig. S5 and S6 in the Online

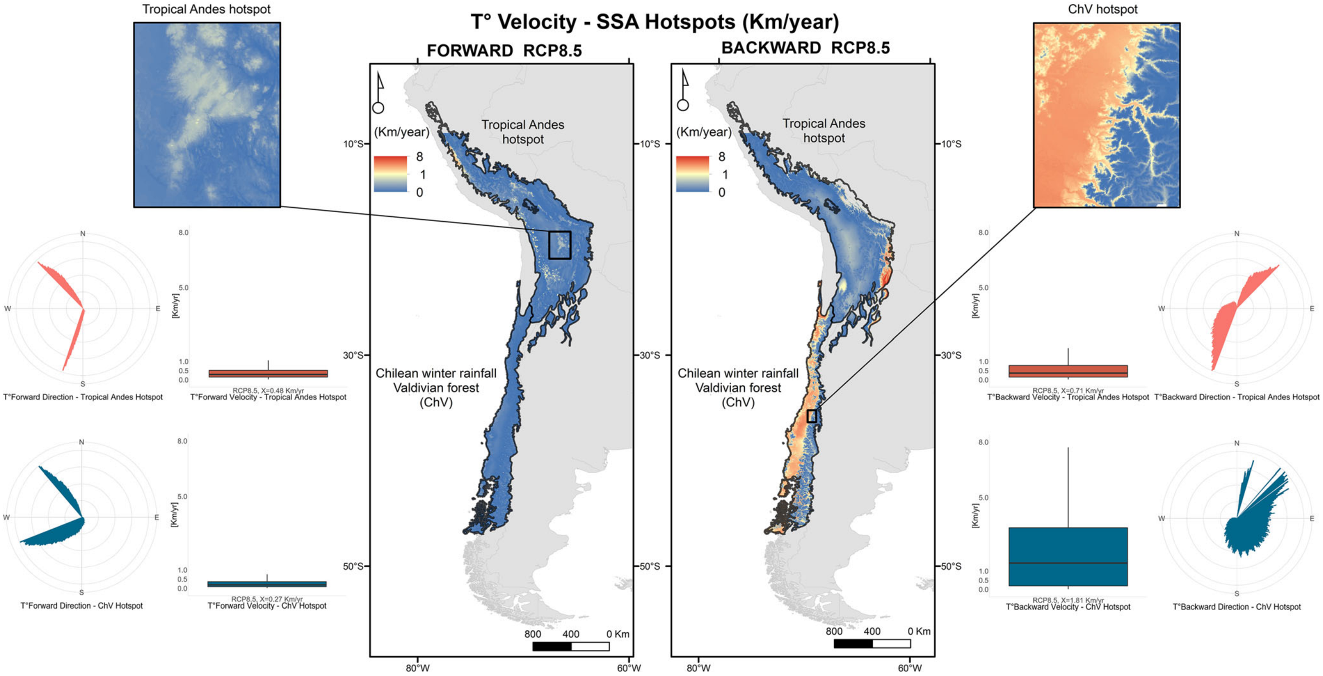

Fig. 3 Spatial climate change velocity patterns for temperature in the SSA hotspots for the RCP8.5-2080 scenario. The center panel shows forward (left) and backward (right) spatial patterns of climate change velocity (in km/year). The histogram plots show the average temperature speed (forward and backward) for the Tropical Andes hotspot (red boxplot) and ChV hotspot (blue boxplot), where the averages are taken over the range of GCMs used and the thick horizontal line represents the median value. The bottom of each box represents the RCP8.5 scenario including the mean value. The vertical line represents the velocity rate in km/year. Histogram plots in polar coordinates show the average temperature direction of change (forward and backward) for the Tropical Andes hotspot (red plots) and ChV hotspot (blue plots). The Tropical Andes hotspot exhibited a common southwest direction between forward and backward estimations. The ChV hotspot exhibited opposite directions, between forward (northwest and southwest) and backward (northeast and southeast) estimations. The two arms on each of these plots represent the main directions observed at each hotspot which are influenced by the Mountain ranges (Andes and Coastal Mountains). Zoom pictures of the spatial pattern of climate change velocity are shown in the upper-left panel for the Tropical Andes hotspot, and in the upper-right panel for the ChV hotspot. See the higher spatial contrast between slower (blue scale, on the eastern side) and faster (red scale) backward velocities at ChV, which are clearly differentiated by the Andes Mountain range

Supplement). According to Carroll's velocity (calculated at the continental level), forward and backward velocity averages were higher in the Tropical Andes hotspot than in the ChV hotspot, showing 3.72 km/year for forward velocity and 4.192 km/year for backward velocity averages. In this study—only considering the HadGEM2-ES model—forward velocity was higher in the Tropical Andes hotspot (0.740 km/year). Conversely, backward velocity was higher in the ChV hotspot (1.74 km/year). The same trend was found considering the velocity average of 31 GCMs. On the striking difference in magnitude between the climate change velocities found by Carroll et al. (2015) and this study, see our Discussion section below.

Hotspot vulnerability to climate change velocity in Southern South America

The magnitude of climate change through SSA hotspots varied according to the variable considered—temperature or precipitation—and to the RCP scenario.

Ecoregions within the Tropical Andes hotspot, such as Central Andean Puna, Central Andean dry Puna, and Central Andean wet Puna, showed a higher linear relation of forward and backward velocity for both variables (temperature and precipitation) in the RCP2.6 scenario (Fig. 4b, d), as well as in the RCP8.5 scenario considering precipitation (Fig. 4c). Forward temperature velocity was higher than backward velocity for the RCP8.5 scenario (Fig. 4a). In the case of the Yungas ecoregions, backward velocity presented the highest rates (Fig. 4). Furthermore, the ChV hotspot and their two ecoregions—Chilean Matorral and the Valdivian Temperate Forests—presented higher backward than forward velocity for temperature and precipitation at both RCP scenarios (Fig. 4a, c). Additionally, the Chilean Matorral presented the highest linear relation of forward and backward velocity for both variables (temperature and precipitation) in the RCP2.6 scenario (Fig. 4b, d, and Table 1).

The vulnerability interpretation of these four quadrants (Fig. 4) suggests threats to sites in the ChV hotspot, with the Chilean Matorral the most threatened under the RCP2.6 scenario (threats to sites and local populations). For the Puna ecoregions, threats to sites and local populations were the most frequent responses. Finally, for the Yungas ecoregions, threats to sites were also identified (Fig. 4b–d).

Table 1 Temperature forward and backward velocity (km/year) in the SSA ecoregions

Code	Forward velocity (km/year)											
	RCP 26 2030			RCP 26 2080			RCP 85 2030			RCP 85 2080		
	Mn	Md	1Q	Mn	Md	1Q	Mn	Md	1Q	Mn	Md	1Q
SD	0.13	0.08	0.06	0.08	0.05	0.03	0.17	0.10	0.07	0.38	0.16	0.09
PY	0.11	0.07	0.05	0.06	0.04	0.03	0.13	0.08	0.06	0.23	0.15	0.07
CDP	0.20	0.14	0.09	0.12	0.08	0.05	0.25	0.17	0.11	0.52	0.39	0.23
CP	0.16	0.10	0.07	0.10	0.06	0.04	0.22	0.14	0.09	0.54	0.35	0.18
CWP	0.19	0.11	0.07	0.12	0.07	0.04	0.26	0.15	0.08	1.03	0.46	0.28
BY	0.12	0.08	0.06	0.07	0.05	0.03	0.14	0.09	0.06	0.23	0.18	0.11
BDF	0.11	0.07	0.06	0.07	0.05	0.03	0.13	0.09	0.06	0.27	0.21	0.12
SY	0.12	0.09	0.06	0.07	0.05	0.04	0.15	0.10	0.07	0.24	0.19	0.11
AD	0.18	0.15	0.10	0.12	0.10	0.06	0.24	0.19	0.13	0.39	0.34	0.22
SS	0.09	0.06	0.05	0.05	0.04	0.03	0.11	0.08	0.06	0.24	0.12	0.08
ChM	0.13	0.09	0.06	0.08	0.06	0.04	0.16	0.12	0.07	0.26	0.22	0.13
HM	0.12	0.08	0.06	0.07	0.05	0.04	0.14	0.10	0.07	0.16	0.13	0.09
LM	0.71	0.58	0.30	0.44	0.36	0.19	0.97	0.78	0.41	1.04	0.87	0.56
VF	0.11	0.06	0.05	0.07	0.04	0.03	0.14	0.07	0.05	0.27	0.17	0.07
PS	0.42	0.22	0.10	0.26	0.14	0.07	0.56	0.31	0.15	0.80	0.65	0.33
MF	0.10	0.06	0.05	0.06	0.04	0.03	0.12	0.07	0.05	0.22	0.14	0.06

Code	Backward velocity (km/ year)											
	RCP 26 2030			RCP 26 2080			RCP 85 2030			RCP 85 2080		
	Mn	Md	1Q	Mn	Md	1Q	Mn	Md	1Q	Mn	Md	1Q
SD	0.37	0.08	0.06	0.24	0.05	0.04	0.50	0.10	0.07	0.79	0.21	0.09
PY	0.28	0.07	0.05	0.13	0.04	0.03	0.33	0.08	0.06	0.28	0.11	0.06
CDP	0.57	0.37	0.12	0.33	0.23	0.08	0.68	0.49	0.17	0.69	0.63	0.36
CP	0.25	0.12	0.07	0.15	0.08	0.04	0.32	0.16	0.09	0.41	0.31	0.16
CWP	0.26	0.09	0.06	0.15	0.06	0.04	0.31	0.12	0.07	0.30	0.18	0.10
BY	1.34	0.10	0.06	0.84	0.07	0.03	1.66	0.13	0.06	0.81	0.29	0.10
BDF	0.24	0.08	0.06	0.16	0.05	0.03	0.31	0.10	0.06	0.69	0.36	0.17
SY	0.55	0.15	0.06	0.39	0.11	0.04	0.76	0.21	0.08	2.77	1.85	0.31
AD	0.39	0.22	0.11	0.26	0.14	0.07	0.54	0.30	0.15	1.65	1.09	0.48
SS	0.24	0.07	0.05	0.11	0.04	0.03	0.22	0.08	0.06	0.23	0.14	0.07
ChM	0.73	0.21	0.07	0.48	0.16	0.04	1.06	0.37	0.09	2.32	2.49	0.50
HM	0.48	0.18	0.06	0.31	0.12	0.04	0.66	0.27	0.08	2.00	0.86	0.23
LM	1.79	1.24	0.56	1.15	0.85	0.39	2.65	1.95	0.94	4.18	4.39	2.88
VF	0.47	0.08	0.05	0.31	0.05	0.03	0.67	0.11	0.05	1.54	0.86	0.13
PS	0.67	0.44	0.16	0.43	0.29	0.11	0.95	0.66	0.25	1.96	1.80	0.91
MF	1.00	0.14	0.05	0.68	0.17	0.03	1.34	0.32	0.05	2.29	2.40	0.68

Ecoregion code: *SD*, Sechura Desert; *PY*, Peruvian Yungas; *CDP*, Central Andean dry Puna; *CP*, Central Andean Puna; *CWP*, Central Andean wet Puna; *BY*, Bolivian Yungas; *BDF*, Bolivian montane dry forests; *SY*, Southern Andean Yungas; *AD*, Atacama Desert; *SS*, Southern Andean steppe; *ChM*, Chilean Matorral; *HM*, High Monte; *LM*, Low Monte; *VF*, Valdivian temperate forests; *PS*, Patagonian steppe; *MF*, Magellanic subpolar forests. Statistics: *Mn*, mean; *Md*, median; *1Q*, 1st quantile

Finally, the relationship between protected area size and forward and backward velocity presented different responses along hotspots and ecoregions (Fig. 5). Forward velocities did not show a clear relationship with protected area size in either one of the ecoregions; however, backward velocities showed either a positive or negative relation with protected area size depending on the hotspot. Protected areas in the Tropical Andes hotspot exhibited a higher vulnerability when the protected area size increased, and the ChV hotspot showed higher vulnerability in smaller protected areas. These trends were similar for both temperature and precipitation velocity calculations.

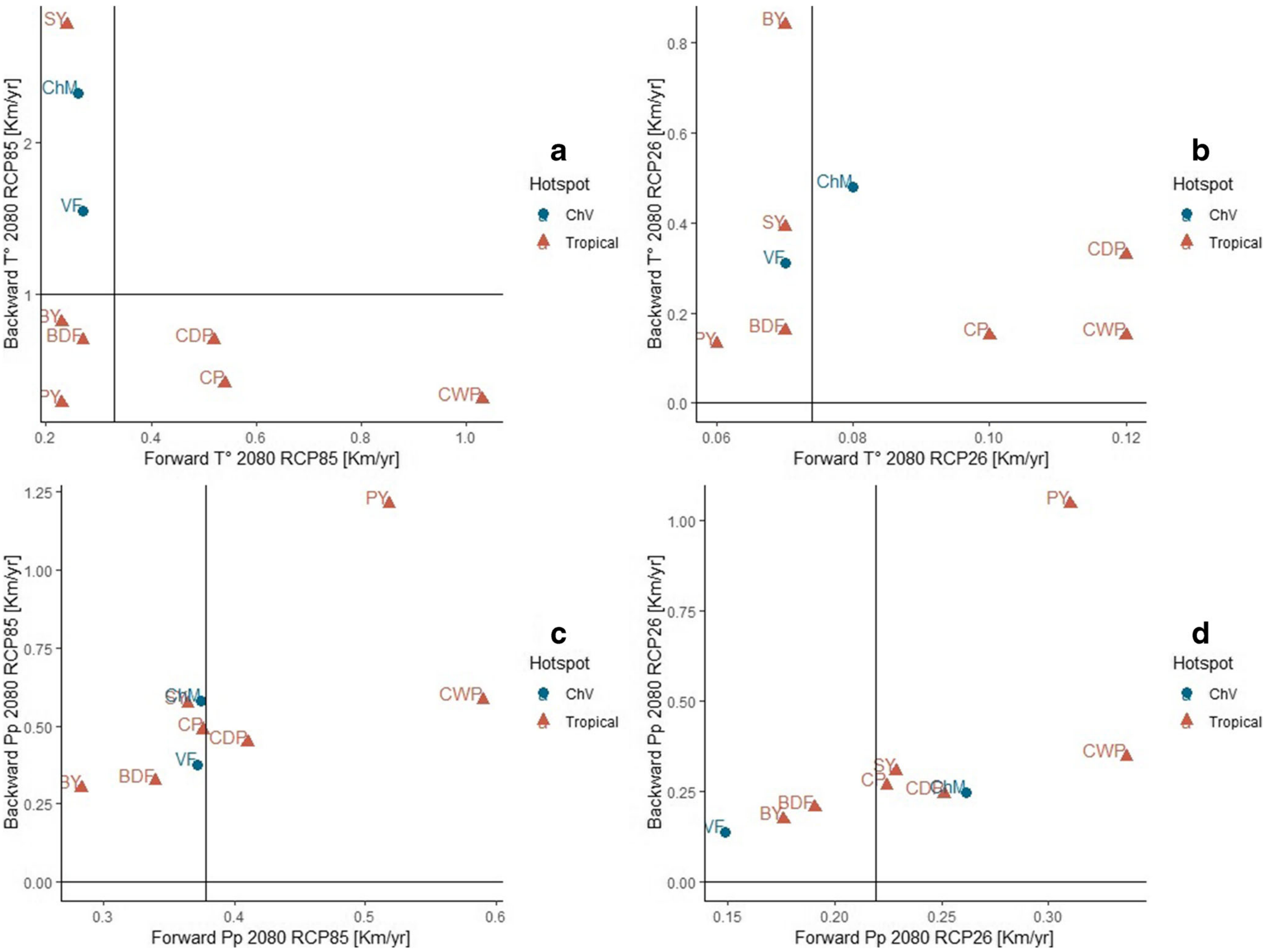

Fig. 4 Vulnerability scheme applied to analyze forward and backward velocity of temperature and precipitation variables. Four plots are shown for the Tropical (red triangles) and the ChV hotspot (blue triangles), where the limits of quadrants are drafted by the median: **a** forward and backward temperature velocity for the RCP8.5 2080 scenario, **b** forward and backward precipitation velocity for the RCP8.5 2080 scenario, **c** forward and backward temperature velocity for the RCP2.6 2080 scenario, and finally **d** forward and backward precipitation velocity for the RCP2.6 2080 scenario. The ecoregion codes are described as follows: (PY) Peruvian Yungas, (CDP) Central Andean dry Puna, (CP) Central Andean Puna, (CWP) Central Andean wet Puna, (BY) Bolivian Yungas, (BDF) Bolivian montane dry forests, (SY) Southern Andean Yungas, (ChM) Chilean Matorral, (VF) Valdivian temperate forests

Discussion

Climate change velocity analysis contribution for Southern South America

Anthropogenic climate change has caused widespread changes in climate conditions during the last century, and more rapid rates of change are expected to occur in the next decades (IPCC 2014, 2018). Such changes are expected to be faster than the changes to which terrestrial ecosystems have been exposed before (Diffenbaugh and Field 2013).

In this study, we evaluated the vulnerability of terrestrial ecosystems to climate change velocity in the SSA ecoregional system, and we found that forward velocity was higher at the Tropical Andes hotspot than at the ChV hotspot, for both climatic variables analyzed (temperature and precipitation). Additionally, backward velocity was higher at the ChV hotspot for the temperature variable.

Vulnerability analysis of climate change velocity allows us to identify differences in the more relevant threats between hotspots. We identified a higher threat for sites than for species and an inverse relation between protected area size and backward velocities for the ChV hotspot. These findings improve the results of climate change velocity conservation implications reported previously for SSA, at global (Loarie et al. 2009) and regional scale (Carroll et al. 2015).

Our regional results compared with Carroll's velocity calculations for SSA (Carroll et al. 2015) featured spatial differences for temperature velocity in each hotspot, being the forward and backward velocity rates higher in the Tropical Andes hotspot than they were in the ChV hotspot. Comparatively, in our study, average

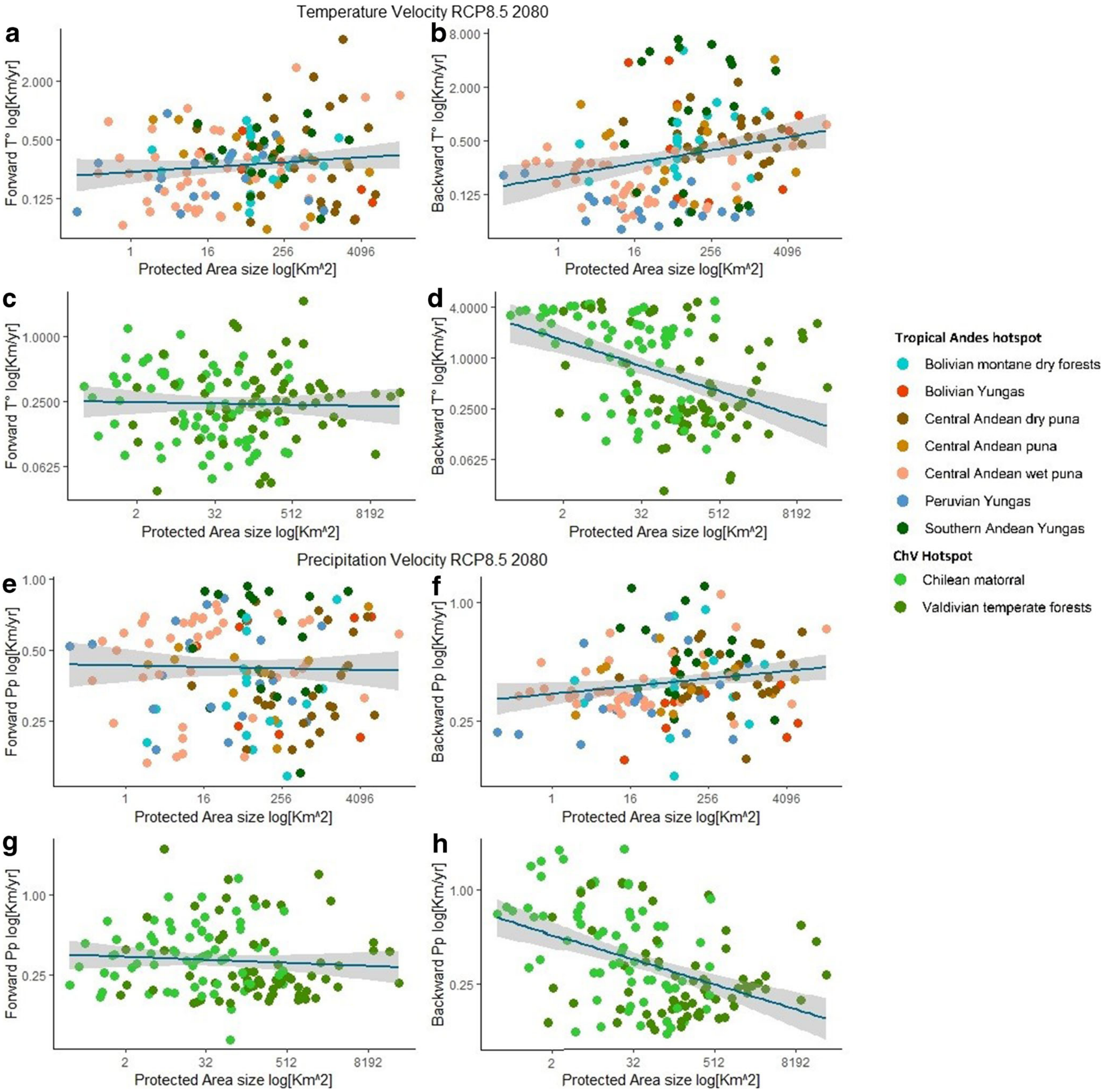

Fig. 5 Protected area size versus climate change velocity. Four linear regressions are shown by each climate variable: temperature velocity in the upper four panels (charts **a**, **b**, **c**, **d**), and precipitation velocity in the four lower panels (charts **d**, **e**, **f**, **g**). Each linear regression indicates the protected area size (x-axis) and climate velocity (y-axis) with a logarithmic scale. Protected areas are differentiated by the groups of ecoregions in each hotspot Tropical Andes hotspot as heat point colors (in upper chart of each part of the figure, i.e., charts **a**, **b**, **e**, **f**), ChV hotspot as green point colors (in lower chart of each part of the figure, i.e., charts **c**, **d**, **g**, **h**)

velocity values were lower in magnitude than Carroll's results, and backward velocity was higher in the ChV hotspot than the Tropical Andes hotspot in a pessimistic scenario. Carroll et al.'s (2015) study was done at the continental level, considering all of north, central, and south America. From this perspective, our findings recall the importance of *regional* climate change evaluations to inform conservation decisions, and of preserving sites to face climate change in key areas in the ChV hotspot.

When we compare our results with future species and ecosystem distribution models reported in SSA areas (e.g. Pliscoff et al. 2012; Swenson et al. 2012; Bambach et al. 2013; Tovar et al. 2013; Ramirez-Villegas et al. 2014; Alarcón and Cavieres 2015; Fuentes-Castillo et al. 2019), we can find new emergent situations. One of them is the overlapping areas between forward velocity identified in this study, and species range contraction areas reported previously. These combinations can be interpreted as priorities for the establishment of conservation area networks under climate change (Carroll et al. 2017), because the combination of faster forward velocities and species/ecosystem range contraction show more urgent priority sites that could be incorporated within a climate-smart conservation network (Nadeau et al. 2015). The combination of scenarios of rapid forward velocity and upward direction could increase the threat for many taxa, especially in the case of species with low dispersal capacities in the most vulnerable ecoregions of the Tropical Andes hotspot (central Andes wet and dry Puna), where altitudinal gradient decreases the area available to find suitable conditions in the future.

In fact, the main effect of mountain heterogeneous landscapes—such as the main landscapes in SSA—will be to slow climate velocity, and lowland homogeneous landscapes will increase climate velocity (Loarie et al. 2009; Diffenbaugh and Field 2013; Dobrowski et al. 2013). However, heterogeneous terrain landscapes, especially in mountain areas, can have areas where climate trajectories traverse dissimilar climates and species must follow paths that minimize their exposure. Thus, the required velocity can have an opposite rate than a climate velocity obtained by a Euclidian distance-based approach (Dobrowski and Parks 2016).

Nevertheless, mountain areas can also exhibit larger flat terrains, such as plateau systems (highlands) that will present faster cores of climate velocity. In this case, the tropical Andes hotspot presents a large plateau system (such as the Puna ecoregion) that exhibited faster climate velocity cores. On the contrary, the ChV hotspot is completely shaped by heterogeneous mountain chains and without these plateau systems. These differences in geographic space will impact habitat availability of micro and macro refugia that could facilitate species persistence under climate change (Ashcroft 2010; Slavich et al. 2014; Carroll et al. 2017; Michalak et al. 2018).

In the tropical Andes, the direction of climate change identified in this study coincides with those reported previously for species and ecosystems, in which an upward movement for high conservation value species and ecosystems has been forecasted due to climate change (Feeley et al. 2011; Ramirez-Villegas et al. 2014). In the case of the ChV hotspot, the direction of climate change exhibited southward movement, which has also been showed for main vegetation formations (Pliscoff et al. 2012) and for plant species under climate change projections (Fuentes-Castillo et al. 2019), especially those inhabiting lowland areas.

Final considerations

This evaluation is based on velocity gradients given by two climate variables (temperature and precipitation). However, these results must be taken cautiously, considering that species and ecosystems may respond differently to rainfall and temperature gradients (Parmesan 2006). Our findings are based on univariate climate change velocities (Hamann et al. 2015) derived from average values of temperature and precipitation in each ecoregion, so the results have been interpreted at the ecoregional level avoiding conclusions at the level of species. It is expected to be an initial baseline for the study of the response in terms of movement of geographic distributions of ecosystems in the study area. Further analyses should incorporate new approaches that allow analyzing the multivariate climate effect of velocity at the species level. For example, recent methodological approaches allow the incorporation of multiple variables in climate velocity analyses (Guerin et al. 2018), allowing to connect species composition with movement gradients. Another element of the analysis that should be analyzed with caution is the effect of pixel size. This is especially relevant in some ecoregions of the study area that are dominated by an extremely diverse topography (Hamann et al. 2015). Many of the altitudinal gradients relevant to regional scale movement may not be represented with a resolution of analysis of 1 km. However, our study shows that velocity of movement in mountainous areas is lower than in flat areas, which should ameliorate the effect of altitude gradients. In addition, the values presented here are averages at the ecoregional scale, so fewer conclusions can be drawn for more restricted sites. By using only two climate variables to quantify velocity gradients, the intrinsic variability present in each ecoregion has a very relevant biological effect. A change in rainfall of (say) 20 mm/year in a hyper-arid desert environment has greater biological effect than the same amount in a tropical forest. The analysis of average values could mask these variations, but it allows their inter-ecoregional comparison.

Conservation implications

This study shows a methodological advance by using regional climatic data to improve the accuracy of predictions, compared with global data. This is especially important for landscapes with high environmental heterogeneity such as SSA. Furthermore, several rapid change areas are expected along the two SSA hotspots and these findings may add important information to determine conservation planning in the region.

As backward velocity describes the isolation degree that a site will experience under climate change (Carroll et al. 2015), this metric was identified as being more relevant in the ChV hotspot, while at the same time, we found an inverse relation between protected area size and backward velocity. The status of the Chilean Matorral has been remarked to have several conservation issues associated with land use intensity (Echeverria et al. 2006; Schulz et al. 2010), insufficient protected areas (Pliscoff and Fuentes-Castillo 2011), high susceptibility to anthropogenic forest fire events (Urrutia-Jalabert et al. 2018), and the rapid spread of exotic species (Fuentes et al. 2015). Protected areas in this ecoregion are not only scarce but small in area (Pliscoff and Fuentes-Castillo 2011) and surrounded by exotic tree plantations, agriculture, and urban developments (Armesto et al. 2010; Miranda et al. 2017). National parks and reserves are concentrated mainly in the Andes Mountain ranges (Pliscoff and Fuentes-Castillo 2011). For the ChV, the availability of protected areas to the south of the hotspot could buffer the effects of the higher velocities of change in lowland areas.

On the other hand, forward velocity interpretation as a stand-alone climatic evaluation and without considering species data (Brito-Morales et al. 2018) describes the exposure of species that are climatically adapted to a site in the present. This metric was identified as more relevant in the Tropical Andes hotspot, in which protected area size is positively correlated with vulnerability. Protected areas within this hotspot also present several conservation issues, especially due to anthropogenic pressures (Hoffmann et al. 2011), where climate change can make conservation efforts more complex (Ramirez-Villegas et al. 2014; Bax and Francesconi 2019). Additionally, threatened species may not be well represented in the current protected areas according to climate change forecasts (del R Avalos and Hernández 2015).

New conservation planning approaches need to incorporate these synergies between metrics to be more effective in the face of biodiversity impacts of climate change. Some recent examples demonstrating this approach could be applied using different metrics, data inputs, and spatial scales (Nadeau et al. 2015; Carroll et al. 2017; Malakoutikhah et al. 2018), thus providing more tools and options to build conservation network areas that would be more resilient under climate change scenarios.

Our results have provided conservation implications for terrestrial ecosystems in SSA hotspots considering climate change velocity, especially in protected areas. However, further research should focus on species responses to climate change in these hotspots; it will be helpful to understand how biodiversity can be affected by climate change exposure.

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