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RESEARCH ARTICLE

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Using near-ground leaf temperatures alters the projected climate change impacts on the historical range of a floristic biodiversity hotspot

Brittany T. Trew[1] | Regan Early[2] | James P. Duffy[1] | Steven L. Chown[3] | Ilya Maclean[1]

[1]Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall, UK

[2]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall, UK

[3]School of Biological Sciences, Monash University, Melbourne, Victoria, Australia

Correspondence
Brittany T. Trew, Environment and Sustainability Institute, University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9FE, UK.
Email: bt302@exeter.ac.uk

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Abstract

Aim: Species distribution models (SDMs) have been used widely to predict the responses of species to climate change. However, the climate data used to drive these models typically represents ambient air temperatures, derived from measurements taken 1–2 m above the ground. Most plant species live near the ground where temperatures can differ significantly, owing to the effects of solar radiation and reduced wind speed. Here, we investigate differences in spatio-temporal patterns in near-ground leaf and ambient air temperatures and the implications this has on projected changes in species richness of a suite of Fynbos plant species.

Location: Fynbos Biome, South Africa.

Methods: For each individual plant species (n = 83), we constructed two types of SDMs: one using ambient air temperatures and one using near-ground leaf temperatures. Each of these models was fitted to species occurrence data for a recent time period and projected backwards into the past. Species richness projections for both time periods were then constructed using binarized projections.

Results: We found that the impact of climate change on species richness – both the degree of suitable climate lost from the historical range and gained outside of the historical range – was greater using SDMs built with near-ground leaf temperatures. Independent validation of the hindcast projections revealed near-ground SDMs to be more accurate.

Main Conclusions: Our study suggests that SDMs constructed using ambient air temperatures are likely overestimating the breadth of the species' occupied thermal niche, thus underestimating the climate change-driven risk to species where near-ground leaf and ambient air temperatures are particularly decoupled from one another. Additionally, ambient air SDMs may be underestimating the ex-situ refugial potential of inland mountains. Ambient air temperatures should not be considered an effective surrogate for investigating climate change impacts on species living near the ground.

KEYWORDS
biodiversity hotspots, climate change, conservation, mediterranean-type biome, microclimate, mountains, refugia, species distribution models

1 | INTRODUCTION

Anthropogenic climate change is predicted to have far-reaching consequences for biodiversity across the globe (Lenoir et al., 2020; Parmesan & Yohe, 2003). Over the last 20 years, species distribution models (SDMs) have emerged as the most widely used method for predicting how species will respond to future climate change (Elith & Leathwick, 2009; Santini et al., 2021; Thomas et al., 2004; Tingley & Beissinger, 2013). These models determine a species' environmental niche, by relating abiotic conditions, often climate, to species occurrences in space (Araújo & Guisan, 2006; Guisan & Thuiller, 2005), and thus make inferences on whether a location is suitable for a species under present, past, and/or future climatic conditions (Kearney & Porter, 2004, 2009). SDMs are typically constructed using climate data interpolated from measurements obtained by weather stations (Lembrechts et al., 2018, 2020) and then projected into the future using projections of the same climate variables. However, weather stations record air temperatures inside well-ventilated protective shields placed 2 m above the ground in open habitats, at locations carefully selected to be unaffected by local microclimatic influence (Bramer et al., 2018; Maclean et al., 2021). We term this measure "ambient temperature." In contrast, many plants and animals experience thermal conditions close to the ground which can be substantially different from those obtained by weather stations (Aalto et al., 2018; Barry & Blanken, 2016; Campbell & Norman, 2012; Körner & Hiltbrunner, 2018), primarily owing to absorption and emittance of radiative energy by the ground.

Radiation from the sun passes through air without appreciably changing its temperature, but the Earth's surface absorbs this radiation and consequently heats up. Some of this heat is exchanged with the air immediately above it via a process of turbulent convection such that the air near the ground is often considerably warmer than at the height of a standard weather station (Barry & Blanken, 2016; Campbell & Norman, 2012). At night the converse is true. The Earth's surface emits radiation and therefore typically becomes cooler than the air, but also cools the air immediately above the ground. This is particularly pronounced under clear sky conditions, when less of the emitted radiation is absorbed and re-emitted back downwards from the sky (Campbell & Norman, 2012). Consequently, diurnal and seasonal changes in near-ground temperatures tend to be greater than those of ambient air. At lower latitudes, the sun is on average closer to its zenith and therefore the flux density of solar radiation reaching the Earth's surface is greater near the equator and the difference between near-ground and ambient temperatures is even more pronounced.

The expected difference in ground and ambient air temperatures across space has a direct bearing of the ability of an SDM to forecast accurately the consequences of warming temperatures on organisms living near the ground (Lembrechts et al., 2018). It is usually the case that SDMs rely on a "space for time" substitution whereby models are constructed using spatial data and projected through time. However, temperature gradients near the ground have the potential to be greater than at ambient air height (Lenoir et al., 2017). This is particularly true in open Mediterranean-type biomes, with limited shading (Rundel et al., 2016).

On the other hand, the leaves of plants tend not to exhibit the same temperature extremes as near-ground temperatures. Temperatures are highest in sunny conditions, but under these conditions, the stomatal apertures of leaves open and they undergo greater evapotranspiration (Michaletz et al., 2015). It is also the case that as leaf temperature increases, its effective vapour pressure increases and a stronger vapour gradient is maintained, also enhancing evapotranspiration (Monteith & Unsworth, 2013). Since greater evapotranspiration results in a cooling effect, leaves have the potential to act as partial homeotherms (Michaletz et al., 2015). In contrast, at night, dew settles on the leaves and resultantly their temperature does not readily drop below dewpoint temperature (owing to the latent heat of condensation). For instance, recent field studies of the *Aspalathus linearis* crop (a tea crop plant endemic to the Fynbos region, more widely known as *rooibos*) have shown that the plants use evaporative cooling in the summer months to minimize the effects of temperature extremes on photosynthetic machinery (MacAlister et al., 2020). These self-regulating mechanisms maintain a more stable thermal environment for the plant than exists around it.

Additionally, within Mediterranean-type regions specifically, temperature regimes are generally moderated by the influence of adjacent oceans which can further increase the divergence between near-ground leaf temperatures and ambient air temperatures. The Mediterranean-type Southern African Fynbos Biome inhabits a relatively narrow landmass (Rundel et al., 2016), bordered on all three sides by oceans, and the inland boundary is rarely more than 220 km away from the moderating effect of these oceans (Bradshaw & Cowling, 2014). Offshore and onshore winds have a significant influence on ambient air temperatures in this region (Bradshaw & Cowling, 2014), but the influence of wind on temperatures reduces markedly nearer to the ground whereby the air directly at the surface is almost entirely still (Barry & Blanken, 2016). As a result of local weather patterns and plant physiology, spatial temperature gradients that plants actually experience may be smaller near the ground, especially when measured as leaf temperature instead of as ambient air temperature. Thus, SDMs derived using ambient air temperatures may overestimate the thermal niche of plant species, and so, they are more likely to underestimate the loss of climate suitability in space as a result of changes through time.

Furthermore, rates of climate change are not necessarily the same for ambient and near-ground temperatures (Lembrechts et al., 2019). Changes in wind speeds, soil moisture, and cloud cover – as a result of changes in prevailing weather conditions – can cause the offset between near-ground and ambient air temperatures to vary over time in non-forested habitats (Maclean et al., 2017). Hypothetically, local reductions in cloud cover – the equivalent to increases in incoming radiation – could magnify the difference between near-ground and ambient air temperatures. As such, any local temporal variations in radiation would ultimately change the degree of divergence between the two temperature measures, which would further reduce the effectiveness of ambient air temperatures as a proxy for the environment near the ground. As a result, predicting future species distributions using ambient air temperatures as a surrogate for temperatures near the ground risks inaccurate conclusions about the magnitude and geographical patterns of future species range shifts (Lembrechts et al., 2018).

In this study, we investigate the predicted change in species richness in the Fynbos biome across a 40-year historical period using two different measures of temperature: ambient air temperatures (1–2 m above the ground) and near-ground leaf temperature (the temperatures of the leaves themselves, averaged across the entire leaf and including both the surface and the interior, at 0.05 m above the ground), using characteristic plant species ($n = 83$) of the Fynbos biome. The biome is situated within the Cape Floristic Region, a Mediterranean-type biodiversity hotspot that hosts the greatest concentration of non-tropical, higher plant species globally. The risk of climate change-driven extinction for plant species here is potentially very high owing to its position on a continental margin, such that potential movement poleward in response to a changing climate is inhibited by the presence of the Atlantic and Indian oceans (Allsopp et al., 2014). Studies investigating the effect of near-ground temperatures on climate change projections in non-forested regions have so far been focused on empirical data collected in alpine climates (see: Lembrechts et al., 2019). However, the greatest degree of thermal decoupling between near-ground leaf temperatures and ambient air temperature variables is likely to be seen in regions with hotter climates and open vegetation structures, where the effect of radiation on ground temperatures is strongest and the temperature profiles above ground are more pronounced. The greater the divergence in spatial gradient between near-ground leaf temperatures and ambient air temperatures, the more likely it is that an SDM constructed using ambient air temperatures will lead to erroneous future projections of a species' suitable geographical range. Given that the SDMs here focus on temperature alone, they should not necessarily be interpreted as improved future predictions for the study area, but rather a demonstration of the impact a measure of temperature from a different position in vertical space can have on climate suitability projections. Doing so will add to the substantial body of work (Altwegg et al., 2014; Midgley et al., 2002; Midgley et al., 2003; Sarmento Cabral et al., 2013) which has sought to understand the vulnerability of the Fynbos biome to climate change and develop robust future conservation strategies.

2 | METHODS

2.1 | Study system

The Fynbos Biome (29.875–34.875°S, 17.375–27.125°E), as defined by the South African vegetation map (South African National Biodiversity Institute, 2018), is located on the southwestern tip of South Africa within the Cape Floristic Region biodiversity hotspot (Figure 1). The biome consists, almost entirely, of treeless heathland (Bergh et al., 2014; Specht & Moll, 1983) and so Fynbos plant species almost exclusively inhabit the space below which a standard weather station would be stationed, therefore experiencing near-ground thermal conditions. Consequently, this biome is a model study system for investigating the differences between near-ground leaf and ambient air temperatures, as well as the effects of near-ground leaf temperature variables on the biome's species composition.

2.2 | Climate data and processing

Hourly climate data were obtained from the ERA5 fifth-generation ECMWF atmospheric reanalysis of the global climate, using the single-level surface dataset (Copernicus Climate Change Service (C3S), 2017) at a 0.25° × 0.25° resolution (approximately 24 km^2), for a historic time period (1981–1991) and for a recent time period (2009–2019). The ERA5 climate data combine past climate observations with climate modelling to generate a series of climate variables for atmospheric, land-surface, and sea parameters. The climate variables: (1) air temperature at 2 m, (2) specific humidity at surface, (3) pressure at surface, (4) precipitation rate, (5) U (west to east) wind speed at 10 m, (6) V (south to north) wind speed at 10 m, (7) total cloud cover, and (8) downward solar radiation at surface were extracted for the extent of the Fynbos Biome (South African National Biodiversity Institute, 2018).

These hourly climate variables were used as inputs for the *Microclimf* package (Maclean, 2022) developed for use in the statistical software R 4.0 (R Core Team, 2020). The package contains tools for fast modelling of the mechanistic processes which drive fine-scale variation in temperatures near the ground, building on modelling methods developed in the *microclima* (Maclean et al., 2019) and *microclimc* (Maclean & Klinges, 2021) packages. In this instance, the model was run in daily time increments and then hourly leaf temperatures –at 0.05 m above the ground were derived using the model's interpolation methods. Here, leaf temperature refers to the average temperature of leaves at specified height above ground, computed from the net energy balance in which absorption of radiation by leaves is computed by assuming, following Campbell (1986), that individual leaf angles in aggregate conform to a continuous prolate spheroid distribution. The distribution of leaf angles determines

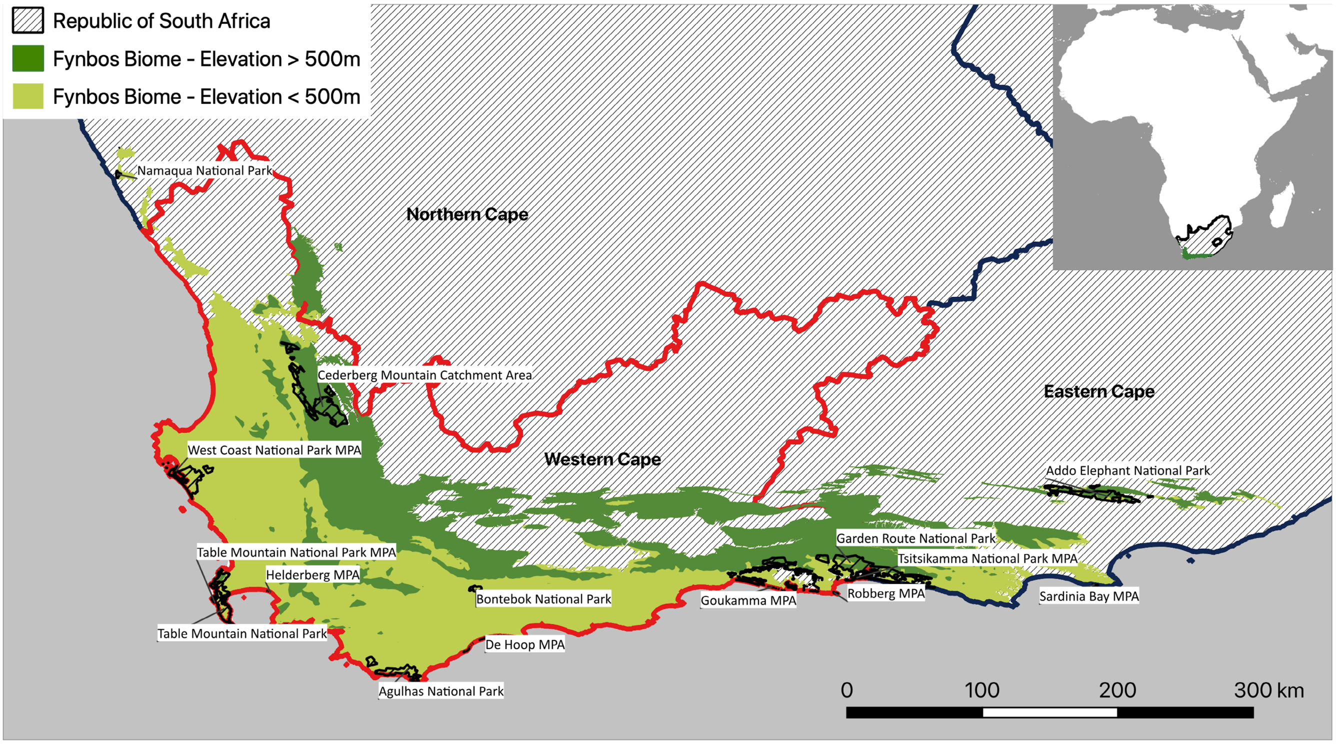

FIGURE 1 The study area encompasses the Fynbos biome (29.875–34.875°S, 17.375–27.125°E) as defined by the South African vegetation map (South African National Biodiversity Institute, 2006–2018), located on the southwestern tip of South Africa within the Cape Floristic Region biodiversity hotspot

both the average amount of radiation absorbed by the surfaces of the leaves and the amount that transmits to lower levels in the vegetated surface. The model was first used to downscale climate to 1 km grid resolution via spatial interpolation and application of an elevation and humidity-dependent lapse rate correction. The model then solves the energy budget equation to derive differences between near-ground and ambient temperature as described in Maclean and Klinges (2021). Radiative energy is assumed to be influenced by slope, aspect, and a leaf area index, the latter assumed to vary seasonally with rainfall, from a minimum of 0.08 to a maximum of 0.81. Sensible heat fluxes are determined from wind speed and properties of the vegetated surface using the method described in Raupach (1994). Wind speed is terrain-adjusted using the method described in Ryan (1977). Latent heat is computed by assuming stomatal conductance varies with photosynthetically active radiation using the method described in Kelliher et al. (1995). Ground heat fluxes are computed assuming moisture-dependent heat storage by the soil, using the method described in Campbell and Norman (2012).

Hourly air temperatures at surface level from the *microclimf* output were validated against hourly air temperatures recorded at the surface level by loggers in 2010 and 2011 (Figure S1–S4) at four separate sites in the Cederberg, Western Cape (see: Braschler et al., 2020). For each grid cell in our study area ($n = 94,374$), at approximately 1 km^2 spatial resolution, daily maximum, daily minimum, and daily mean temperatures were extracted from the hourly *microclimf* output, and the mean for each of our two decadal time periods (1981–1991 and 2009–2019) was calculated for near-ground leaf temperature and for ambient air temperature. Mean daily maximum, mean daily minimum, and mean daily mean near-ground leaf temperatures were used as environmental predictors for species distribution modelling near the ground. Mean daily maximum, mean daily minimum, and mean daily mean temperatures at 2 metres were used as environmental predictors for species distribution modelling at ambient air temperatures. These temperature variables were tested for multicollinearity using pairwise correlation (Figure S5) and variance inflation factor analysis (Table S1). For interpretation purposes, for each grid cell within the study area, the aforementioned temperature variable at ambient air height was plotted against the equivalent value for leaves near the ground. Additionally, change over time was calculated as the difference between mean values for each time period in each grid cell for ambient air and near-ground leaf temperature variables.

2.3 | Biological data and processing

Occurrence data for plant species in the Cape floristic Region are freely available from the Global Biodiversity Information Facility (GBIF; see: www.gbif.org). For this study, we focused on plant species that are considered important and diagnostic of the Fynbos biome (Bergh et al., 2014), and included species from the three major structural component groups: (1) ericoid shrubs, (2) restioid graminoids, and (3) proteoid broadleaved and fine-leaved shrubs. We conducted a search of GBIF for georeferenced occurrence records for species within these component groups and identified 106 species with available occurrence data. Duplicate records in a single grid cell and records outside of the Fynbos Biome area were removed for the present (2009–2019) and historical (1981–1991) time periods and species occurrences recorded in the present time period with <50 occurrences were discounted; 83 species were ultimately included for climate suitability modelling.

Due to there being 43% fewer occurrence data points for the historical period, changes in species distributions were determined by fitting the models using occurrence data for the recent period and then projecting the models backwards in time to derive estimates of species distributions during the historical time period. Within the study area, a random selection of 10,000 background points was used as pseudo-absences, with random sampling repeated 5 times. Ensemble species distribution models for each species were fitted using the *Biomod2* package (Thuiller et al., 2016) in R 4.0 (R Core Team, 2020) separately to leaf temperature variables near the ground (mean daily maximum, mean daily minimum, and mean daily mean temperatures) and to ambient air temperature variables (mean daily maximum, mean daily minimum, and mean daily mean temperatures) from 2009 to 2019. Each ensemble model was calculated as the weighted sum of probabilities of individual model algorithms: generalized linear model (GLM; McCullagh & Nelder, 1983), gradient boosting machine (GBM; Greenwell et al., 2020), artificial neural networks (ANN; Ripley, 1996), classification and regression trees (CTA; Breiman et al., 1984), which were calibrated with presence-absence occurrence data using an 80:20 (training: test) split. The ensemble models for each species were then projected back in time, using leaf temperature variables near the ground and to temperature variables at ambient air height from 1981 to 1991, to predict climate suitability for each species.

The final ensemble projections for the historical time period (1981–1991) were independently evaluated using a continuous Boyce index (Boyce et al., 2002; Hirzel, Lay, Helfer, Randin, & Guisan, 2006) to assess whether the historical projections were reasonable. The indices were calculated with the *Boyce* function (Di Cola et al., 2017) from the *Ecospat* package (Broennimann et al., 2020) in R 4.0 (R Core Team, 2020) with default parameters, using presence-only occurrence data obtained from GBIF for the historical time period. This method derives a predicted-to-expected (P/E) ratio by partitioning climate suitability projections into multiple bins, and for each bin calculating (a) the predicted frequency of evaluation points and (b) the expected frequency of evaluation points, that is, the frequency expected from a random distribution across the study area. Using this index, a low suitability bin is assumed to contain fewer evaluation presences than expected by chance and vice versa. The index varies between −1 and 1. Index values >0 indicate that the projections are consistent with the distribution of presences in the independent evaluation dataset, index values close to zero mean that the model is not different from a chance model, and index values <0 suggest an incorrect model.

In order to illustrate the divergence between species distribution models derived using ambient air with those derived using near-ground leaf temperatures, we produced species richness projections for our suite of species. Binary (presence/absence) models were created from the continuous projections for individual species (once for the ambient air SDM and once for the near-ground leaf SDM) using a species-specific TSS maximization thresholding approach, and these presence/absence projections were summed (Ferrier & Guisan, 2006) to derive two different projections of species richness based on ambient air and near-ground leaf temperatures respectively for the historical time period. Estimates of changes in species richness were then created by subtracting projections of historic species richness from the predictions of species richness for the present time period. Additionally, the historical binary projections of presence and absence for each species were used to quantify the projected change in a species' total range within the study area using the *Biomod2* package (Thuiller et al., 2016) in R 4.0 (R Core Team, 2020); that is, whether a species' predicted binary presence or absence in a given grid cell was stable over time or experienced a loss or gain, assuming no dispersal (excluding grid cell gains) and full dispersal (including grid cell gains) separately between the two time periods.

Finally, we used the *sdm* package (Naimi & Araújo, 2016) in R 4.0 (R Core Team, 2020) to create ecological niche visualizations of the thermal conditions under which our suite of Fynbos species was projected to be present in 2009 to 2019 according to our SDMs, separately for species richness projections created using ambient air temperature variables and those created using near-ground leaf temperature variables.

3 | RESULTS

3.1 | Climate analysis

Across both time periods, mean daily maximum leaf temperatures near the ground were consistently found to be higher (9.5°C higher on average) than the mean daily maximum temperatures at ambient air height (Figure 2). Nevertheless, variance in spatial temperature gradients were found to be considerably greater for mean daily maximum temperatures at ambient air height (1981–1991: 5.6°C and 2009–2019: 6.3°C) than mean daily maximum near-ground leaf temperatures (1981–1991: 1.0°C and 2009–2019: 1.2°C). For every degree of mean daily maximum near-ground leaf temperature variation in space, there is approximately a ~1.8°C variation in mean daily maximum ambient air temperatures (Figure 2a). Specifically, the coldest locations were found to be mountain sites at elevations >500 m, as well as western coastlines. There were high levels of thermal divergence between near-ground leaf and ambient air mean daily maximum temperatures in these areas, as great as ~15°C (Figure S6). Whereas the warmest locations with the highest mean daily maximum temperatures for both measures were found to be concentrated in the coastal lowlands to the west of the biome and in sites inland especially those located in the

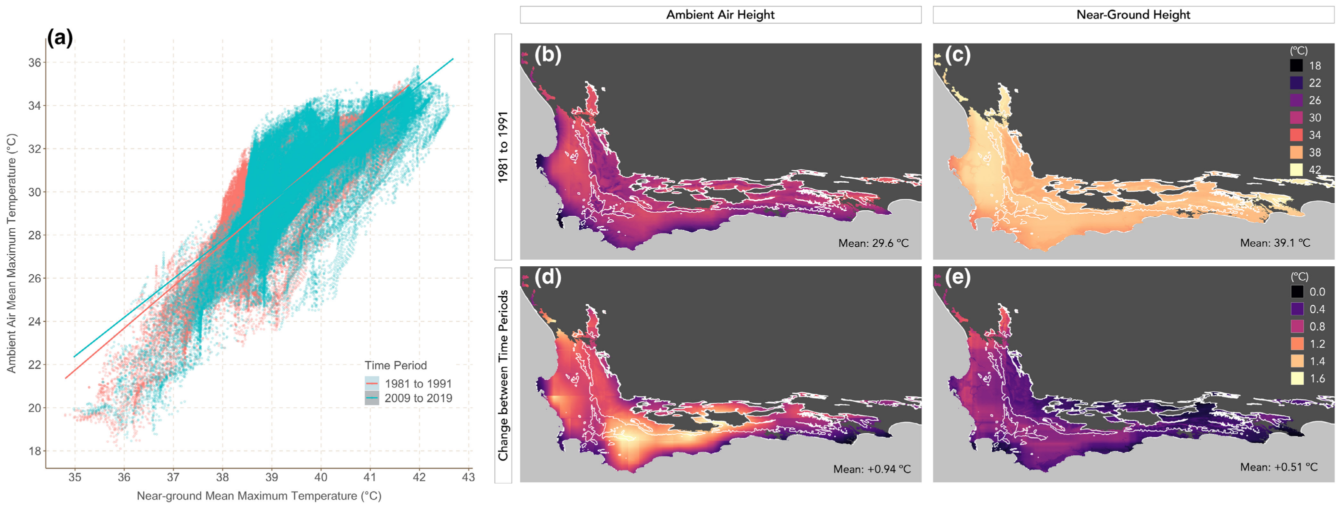

FIGURE 2 (a) Correlation plot of the relationship between ambient air and near-ground mean daily maximum temperatures for each grid cell ($n = 94{,}374$), for the historical (slope = 1.95; intercept = −46.4; $p < .001$; Adjusted R^2 .7) and recent time periods (slope = 1.79; intercept = −40.4; $p < .001$; Adjusted R^2 .6); mean daily maximum temperatures across the Fynbos biome during 1981–1991 at (b) ambient air height and (c) ground level; overall change in mean daily maximum temperatures across the Fynbos biome at (d) ambient air height and (e) ground level. Mountain topography greater than 500 metres above sea level is indicated in the white outlines

northeast of the biome (Figure 2b,c). Thermal divergence between the two different temperature measures was found to be as small as ~7°C here.

From the historical period to the present, mean daily maximum temperatures have increased faster, on average, at ambient air height (+0.94 °C) than for leaves near the ground (+0.51°C). Near-ground daily maximum leaf temperatures are increasing fastest in the northwest and along the western coastline, with some changes also occurring in the central lowlands. There have been minimal changes in daily maximum leaf temperatures in the eastern section of the biome. This contrasts with ambient air temperatures which have increased most significantly in the central section of the biome. The highest rates of change for both measures of temperature were concentrated in the central and northwest sections of the biome, with the slowest rates of change occurring in the eastern section (Figure 2d,e).

The relationship between mean daily minimum leaf temperatures near the ground and ambient air temperatures follows a similar narrative to mean daily maximum temperatures. For every degree of difference in mean daily minimum leaf temperatures across geographical space near the ground, there is a greater than 1°C degree difference in mean daily minimum ambient air temperatures (Figure S7). In other words, there is greater variation across space in mean daily minimum ambient air temperatures than near-ground leaf temperatures. As with the spatial pattern of mean daily maximum temperatures, the lowest mean daily minimum temperatures for both temperature measures were found inland, away from the coastline, particularly concentrated in the western and eastern mountain regions. Mean daily minimum ambient air temperatures increased over twice as fast (+0.55°C) as mean daily minimum leaf temperatures near the ground (+0.25°C). Spatial patterns of change were largely similar, with increases in mean daily minimum temperatures having occurred mostly in the central region (Figure S7). However, there is some divergence in the western mountain and lowland areas where mean minimum leaf temperatures near the ground are increasing at a slower than average rate and ambient air temperatures are increasing at a faster than average rate.

Over the past 40 years, mean daily mean temperatures have risen from the historical period to the present at a similar rate at both ambient air height (+0.77°C) and for leaves near the ground (+0.76°C). Geographical patterns of warming for mean daily mean leaf temperatures near the ground and ambient air temperatures were largely similar, with central interior sites having experienced the highest rates of warming (Figure S8). In contrast, the northwest and easternmost sections of the biome have experienced very little warming and even some cooling.

3.2 | Species distribution models

Model testing, using cross-validation of semi-independent occurrence data, suggested high model accuracy with TSS and ROC scores >0.8 for all species distribution models constructed with ambient air temperatures or constructed with leaf temperatures near the ground (Table S2). SDMs constructed with leaf temperatures near the ground performed marginally better on average for all cross-validation methods. When the hindcast projections were independently tested with historic, presence-only occurrence data, the majority of models scored a Boyce index above 0.5. Models constructed with ambient air temperatures were less accurate overall with 55% of models scoring over 0.5 and a mean score of 0.45, in contrast to models constructed using near-ground leaf temperatures whereby 67% of models scored over 0.5 with a mean score of 0.55 (Table 1). The true difference between the means between ambient

TABLE 1 Boyce Index scores based on independent presence-only data for models constructed with near-ground and ambient air temperatures respectively. Scores for projections created with temperatures near the ground (mean: 0.55) were 0.1 greater on average than scores for projections created with ambient air temperatures (mean: 0.45). Projections created with leaf temperatures near the ground also performed better than ambient air projections 60% of the time

	Boyce index score	
Species	**Near-ground**	**Ambient air**
Agathosma apiculata	0.74	0.61
Agathosma capensis	0.74	0.32
Agathosma mundtii	0.22	0.31
Berzelia abrotanoides	0.45	0.22
Berzelia intermedia	0.86	0.71
Brunia laevis	0.41	−0.56
Brunia paleacea	0.79	0.19
Cliffortia falcata	0.76	0.13
Cliffortia ilicifolia	0.88	0.72
Cliffortia odorata	0.73	0.83
Cliffortia polygonifolia	0.37	0.33
Diastella divaricata	0.62	0.76
Diastella proteoides	0.97	0.44
Erica articularis	0.76	0.32
Erica calycina	0.65	0.44
Erica cerinthoides	0.18	0.48
Erica coccinea	0.56	0.36
Erica cubica	0.18	0.84
Erica curviflora	0.41	0.68
Erica equisetifolia	0.62	0.76
Erica ericoides	0.73	0.08
Erica glandulosa	0.87	0.81
Erica grandiflora	0.25	0.63
Erica hispidula	0.62	0.36
Erica labialis	0.80	0.10
Erica lutea	0.68	0.53
Erica mammosa	0.31	0.53
Erica multumbellifera	0.78	0.73
Erica muscosa	0.63	0.92
Erica nudiflora	0.78	0.38
Erica pulchella	0.78	0.62
Erica sessiliflora	0.82	0.17
Erica sparsa	0.82	0.17
Erica versicolor	0.43	0.73
Erica viscaria	0.72	0.88
Leucadendron eucalyptifolium	0.72	−0.55
Leucadendron gandogeri	0.72	−0.55
Leucadendron lanigerum	0.31	0.69
Leucadendron laureolum	0.58	0.51
Leucadendron levisanus	0.15	0.17
Leucadendron spissifolium	0.79	0.91
Leucadendron uliginosum	−0.43	0.88
Leucadendron xanthoconus	0.68	0.66
Leucospermum calligerum	0.87	0.93
Leucospermum cordifolium	0.83	0.47
Leucospermum hypophyllocarpodendron	0.05	0.34
Leucospermum oleifolium	−0.29	0.58
Leucospermum truncatulum	0.91	0.82
Metalasia acuta	0.65	0.71
Metalasia erubescens	−0.30	−0.49
Metalasia pulcherrima	0.15	0.67
Metalasia pungens	0.62	0.31
Mimetes hirtus	0.93	0.71
Mimetes pauciflora	0.56	0.58
Muraltia alopecuroides	1.00	1.00
Muraltia ericifolia	0.29	0.78
Muraltia satureioides	0.63	−0.60
Paranomus dregei	0.83	0.89
Protea acaulos	0.77	0.75
Protea aurea	0.67	0.88
Protea burchellii	0.48	0.13
Protea compacta	0.28	−0.48
Protea cordata	−0.28	0.20
Protea coronata	0.14	0.69
Protea cynaroides	0.22	−0.16
Protea eximia	0.27	0.87
Protea grandiceps	0.62	0.89
Protea longifolia	0.27	−0.58
Protea lorifolia	0.79	0.81
Protea magnifica	0.62	0.53
Protea obtusifolia	0.63	0.19
Protea punctata	0.76	0.62
Protea scabra	0.70	0.86
Protea scolymocephala	0.90	0.76
Protea speciosa	0.20	−0.14
Serruria elongata	0.68	0.30
Serruria rubricaulis	0.61	−0.37
Stoebe alopecuroides	0.03	0.94
Stoebe capitata	0.54	0.45
Stoebe spiralis	0.64	0.53
Struthiola argentea	0.90	0.75
Struthiola myrsinites	0.76	0.82
Struthiola striata	0.66	0.32

air and near-ground leaf Boyce Index scores was significant and not equal to zero (Welch's *t* test, $t_{82} = -2.0$, $p < .05$). Projections created with leaf temperatures near the ground also performed better than ambient air projections, obtaining a higher Boyce index score 60% of the time. However, it is important to note that both types of models are likely to be overestimating observed species richness for the 1980s when scored against the limited amount of occurrence observations we have for that time period.

Hindcast predictions of species richness models based on ambient air temperatures predicted much higher numbers of species occurring along the northwest and east coastlines, the western peninsula, and inland mountain regions (Figure S9). In contrast, hindcast predictions of species richness models based on near-ground leaf temperatures predicted higher numbers of species occurrence across the western and central lowland plains as well as across northwest mountain regions near the Cederberg Mountain Catchment Area.

The predictions of species richness change between 1980 and 2019, based on the hindcast projections, suggest that models created with near-ground leaf temperatures predict greater reduction of climate suitability within the species' historical range than models created using ambient air temperatures. When we assumed no potential dispersal of species through time (Figure 3), each 1 km^2 grid cell in the Fynbos biome was predicted to lose a median of 3 species and 40% of historical species richness from the 1980s when using ambient air models, and a median of 4 species and 43% of historical species richness using near-ground models. The mean change in species richness assuming no dispersal was significantly higher using near-ground models than ambient air models for both absolute change in species numbers (Welch's *t* test, $t_{96957} = -64.0$, $p < .001$) and percentage change in species numbers (Welch's *t* test, $t_{96957} = -31.7$, $p < .001$). When assuming full dispersal of species through time (Figure 4), each grid cell in the Fynbos biome was predicted to lose a median of 2 species and 25% of species richness when using both ambient air models and near-ground models. However, these full dispersal scenario results are based on significant gains in near-ground climate suitability for Fynbos species in the northeast of the biome. The mean change in species richness assuming full dispersal was significantly higher using near-ground models than ambient air models for both absolute change in species numbers (Welch's *t* test, $t_{96957} = 27.0$, $p < .001$) and percentage change in species numbers (Welch's *t* test, $t_{96957} = 77.0$, $p < .001$). Individual species distribution models predicted less reduction in climate suitability – as the percentage change of grid cells from suitable to unsuitable – for 57 out of 83 species (69%) when ambient air temperatures were used as opposed to models constructed using leaf temperatures near the ground; wherein 26 out of 83 species (31%) predicted less reduction in climate suitability (Table 2). Individually, SDMs constructed using ambient air temperatures predicted an average of 31.6% loss of grid cells with a suitable climate, in contrast to an average of 40.1% loss of grid cells with a suitable climate predicted by models constructed using leaf temperatures near the ground.

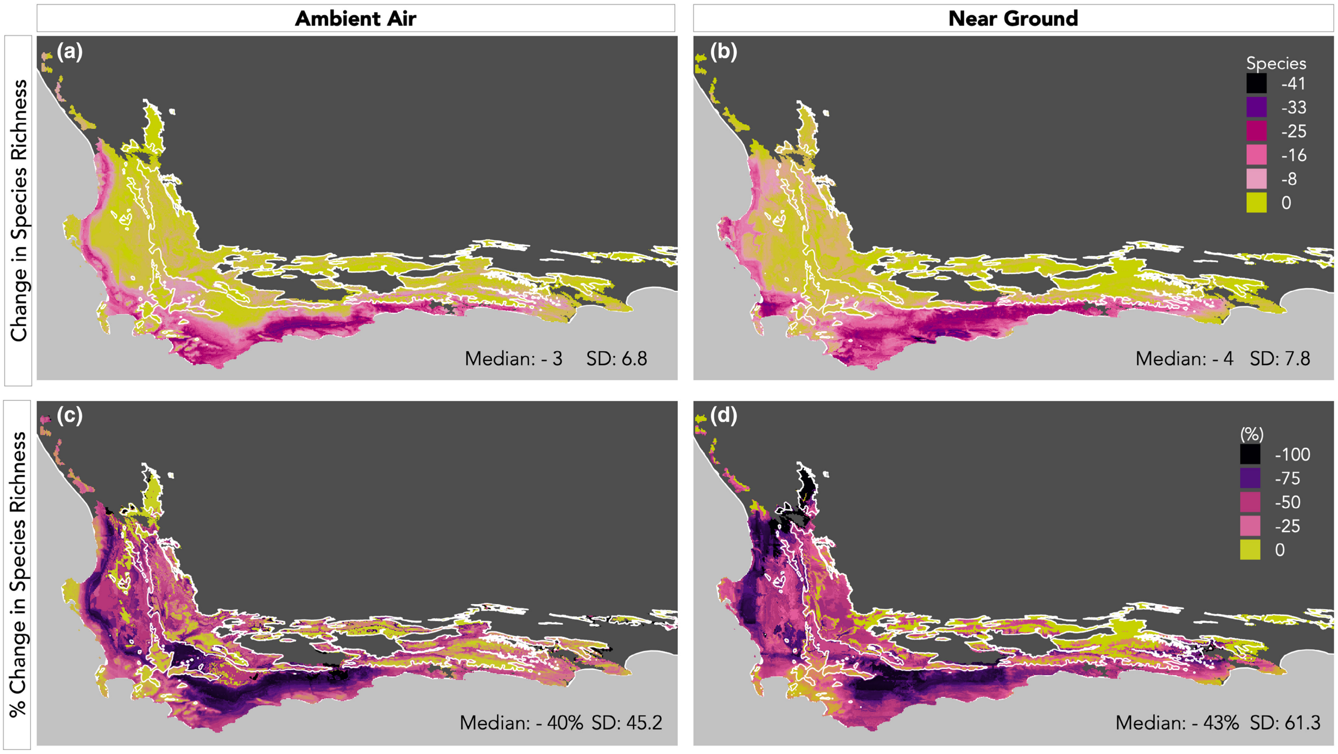

FIGURE 3 (a, b) The **absolute change** in number of species and (c, d) the **percentage change** in number of species ($n = 83$) predicted to be present in each grid cell across the Fynbos biome – using stacked species distribution model projections from individual SDMs constructed with ambient air or near-ground temperatures and **assuming no dispersal** – between 2009–2019 and 1981–1991. Mountain topography >500 m above sea level is indicated in the white outlines

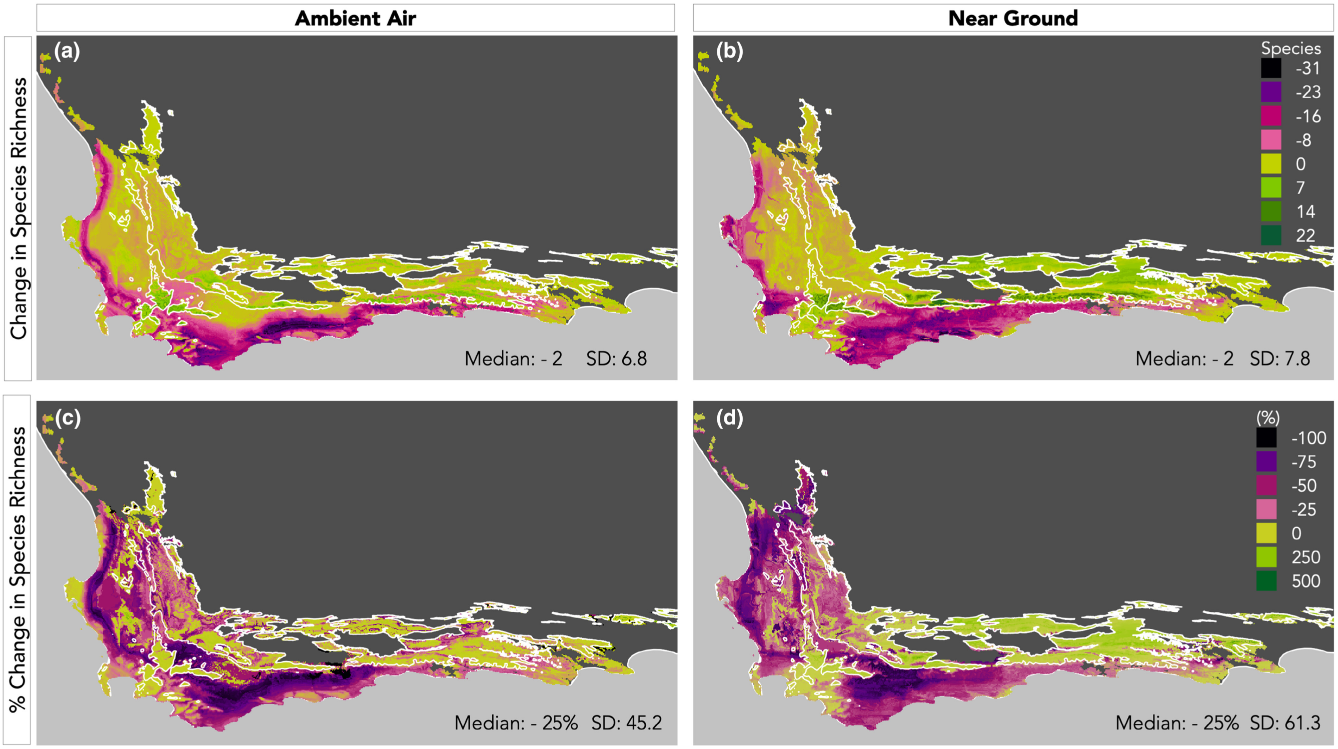

FIGURE 4 (a, b) The **absolute change** in number of species and (c, d) the **percentage change** in number of species (*n* = 83) predicted to be present in each grid cell across the Fynbos biome – using stacked species distribution model projections from individual SDMs constructed with ambient air or near-ground temperatures and **assuming full dispersal** – between 2009–2019 and 1981–1991. Mountain topography >500 m above sea level is indicated in the white outlines

In geographical space, the divergence – measured as the standard deviation between the species richness of projections created with ambient air temperatures and the species richness projections created with near-ground leaf temperatures – in the potential change in species richness from distributions in the 1980s was particularly pronounced along the northwest coastline and lowland plains whereby near-ground models predicted significantly higher levels of climate suitability loss from historical ranges, especially when assuming a no dispersal scenario. Additionally, despite faster rates of climate change at ambient air height in central lowland plains of the Fynbos biome, ambient air SDMs predicted significantly less loss in climate suitability than near-ground SDMs (Figure S10). This pattern is also similar when we assume full dispersal, with near-ground models suggesting that the potential for species range shifts or expansion into this area is unlikely to compensate for the level of climate suitability loss experienced by other species. In mountain locations with elevation greater than 500 metres, models created using ambient air and near-ground leaf temperatures predict similar levels of average species loss when assuming no dispersal of species between time periods (−27% and −28.1% respectively). However, when we assumed full dispersal, SDMs created using near-ground leaf temperatures suggested that there was a significant potential for ex-situ refugia (see: Ashcroft, 2010; Keppel et al., 2012) in these locations, predicting significant gains on average in contrast to ambient air SDMs (+30.9% and −6.1% respectively). Therefore, based on model validation, SDMs built with ambient air temperatures appeared to be underestimating the loss of climate space in our species' historical ranges and underestimating the potential for range shifts in full dispersal scenarios.

According to visualizations of the 2009 to 2019 (Figure 5) predicted temperature niche for our study species, when SDMs are constructed using near-ground leaf temperatures, the majority of species inhabited a significantly narrower, but also much warmer, thermal niche than when SDMs were constructed using ambient air temperatures. According to SDMs using near-ground leaf temperature, species were inhabiting locations with mean maximum temperatures between approximately 35°C and 39°C. In contrast, according to SDMs using ambient air temperatures, species were inhabiting locations with mean maximum temperatures between approximately 19 and 30°C and so these SDMs are overestimating the thermal niche of our study species.

4 | DISCUSSION

This study compares the change in species richness projected by models constructed using ambient air temperatures versus models constructed using leaf temperatures near the ground, with the results suggesting important divergence between the two. We demonstrate that, based on independent validation, projections by models constructed using ambient air temperatures are likely to have underestimated the loss of suitable climate space within our

TABLE 2 Change in climate suitability projected from historical to present time periods for each individual species ($n = 83$) as percentages of total grid cells occupied in 2009 to 2019. Overall mean for suitable climate lost within the historical ranges: **ambient air – 31.6% and near-ground - 40.1%**; Overall mean for suitable climate predicted outside of the historical ranges: **ambient air – 29.8% and near-ground – 462.9%**.

	Suitable climate lost (% of grid cells)		Suitable climate gained (% of grid cells)	
Species	**Ambient air**	**Near ground**	**Ambient air**	**Near ground**
Agathosma apiculata	0.0	37.0	136.9	624.9
Agathosma capensis	5.8	18.1	72.4	0.0
Agathosma mundtii	9.9	14.1	36.6	0.7
Berzelia abrotanoides	34.0	47.0	9.1	8.9
Berzelia intermedia	19.6	0.0	17.6	1819.7
Brunia laevis	45.5	69.5	0.4	0.1
Brunia paleacea	52.1	57.9	1.5	2.8
Cliffortia falcata	18.1	32.9	2.5	15.6
Cliffortia ilicifolia	12.8	28.4	13.4	0.0
Cliffortia odorata	27.0	45.1	0.5	2.8
Cliffortia polygonifolia	55.6	75.9	1.7	0.0
Diastella divaricata	56.3	30.1	0.3	1.0
Diastella proteoides	16.8	0.0	16.5	110.4
Erica articularis	52.4	61.9	0.7	0.0
Erica calycina	51.6	59.3	0.0	0.0
Erica cerinthoides	15.8	6.2	3.3	23.4
Erica coccinea	33.7	40.5	0.5	1.5
Erica cubica	0.1	72.8	81.8	91.1
Erica curviflora	38.9	40.5	5.0	11.3
Erica equisetifolia	20.4	49.8	5.2	6.7
Erica ericoides	23.0	35.0	0.0	1.4
Erica glandulosa	0.3	1.0	82.4	513.9
Erica grandiflora	55.7	75.9	0.6	6.8
Erica hispidula	28.3	37.6	6.3	6.5
Erica labialis	49.8	57.2	14.2	3.5
Erica lutea	37.1	56.0	1.0	0.1
Erica mammosa	60.1	48.5	1.3	0.0
Erica multumbellifera	41.2	56.4	3.2	1.1
Erica muscosa	48.6	58.4	9.7	3.4
Erica nudiflora	54.6	48.3	4.4	3.5
Erica pulchella	45.3	2.8	0.0	19.6
Erica sessiliflora	25.7	16.6	1.0	21.1
Erica sparsa	2.0	0.0	169.5	18161.4
Erica versicolor	0.8	4.5	48.4	46.0
Erica viscaria	57.6	59.2	0.3	0.5
Leucadendron eucalyptifolium	0.0	11.8	104.7	812.0
Leucadendron gandogeri	64.1	70.4	0.2	1.1
Leucadendron lanigerum	78.6	82.5	36.7	25.8
Leucadendron laureolum	26.8	41.5	3.0	0.0
Leucadendron levisanus	40.3	45.7	0.0	0.0
Leucadendron spissifolium	30.8	42.2	0.0	24.1
Leucadendron uliginosum	4.9	0.0	25.0	2376.2

(Continues)

TABLE 2 (Continued)

Species	Suitable climate lost (% of grid cells)		Suitable climate gained (% of grid cells)	
	Ambient air	Near ground	Ambient air	Near ground
Leucadendron xanthoconus	42.5	67.6	0.1	0.5
Leucospermum calligerum	12.2	36.4	3.6	2.6
Leucospermum cordifolium	45.8	53.8	0.9	0.4
Leucospermum hypophyllocarpodendron	52.6	43.7	7.3	0.3
Leucospermum oleifolium	21.9	56.9	4.4	2.7
Leucospermum truncatulum	42.2	73.6	0.8	0.8
Metalasia acuta	32.0	25.7	12.3	27.0
Metalasia erubescens	49.8	82.8	1.3	0.5
Metalasia pulcherrima	0.0	3.8	1127.0	1721.0
Metalasia pungens	31.7	6.8	0.0	849.1
Mimetes hirtus	51.5	59.7	0.8	0.9
Mimetes pauciflora	11.7	64.3	42.5	5817.9
Muraltia alopecuroides	9.7	0.1	0.0	36.6
Muraltia ericifolia	19.7	1.1	0.0	356.7
Muraltia satureioides	26.2	0.7	1.7	90.4
Paranomus dregei	22.3	18.0	31.9	160.6
Protea acaulos	60.5	46.3	1.1	11.5
Protea aurea	71.7	33.2	47.2	11.0
Protea burchellii	71.0	89.9	1.6	19.8
Protea compacta	16.8	73.4	1.4	0.2
Protea cordata	30.1	71.5	3.9	0.0
Protea coronata	8.8	24.1	23.1	25.1
Protea cynaroides	17.0	17.5	1.8	39.4
Protea eximia	9.1	35.3	20.3	36.7
Protea grandiceps	22.3	61.6	1.1	0.0
Protea longifolia	33.3	72.6	0.7	0.0
Protea lorifolia	0.4	35.2	28.2	137.0
Protea magnifica	42.9	49.3	0.0	1.1
Protea obtusifolia	30.1	46.6	0.2	0.0
Protea punctata	40.8	73.4	0.0	185.7
Protea scabra	30.8	45.2	8.5	6.4
Protea scolymocephala	55.0	55.7	1.7	3.0
Protea speciosa	23.9	36.6	7.9	14.5
Serruria elongata	31.8	61.0	2.7	0.1
Serruria rubricaulis	38.7	57.7	1.7	0.0
Stoebe alopecuroides	3.3	0.0	29.2	3635.1
Stoebe capitata	75.8	55.5	53.3	0.0
Stoebe spiralis	32.9	40.1	2.2	14.4
Struthiola argentea	0.0	0.0	59.6	431.2
Struthiola myrsinites	18.2	0.0	21.4	33.2
Struthiola striata	44.6	12.8	0.0	2.4

species' historical ranges by overestimating the breadth of a species' thermal niche and assuming a greater temperature gradient in space (supporting similar conclusions by Lembrechts et al., 2019). As a result, even though ambient air temperatures have increased at a faster rate than near-ground leaf temperatures, the increases in leaf temperatures near the ground that have occurred are likely to

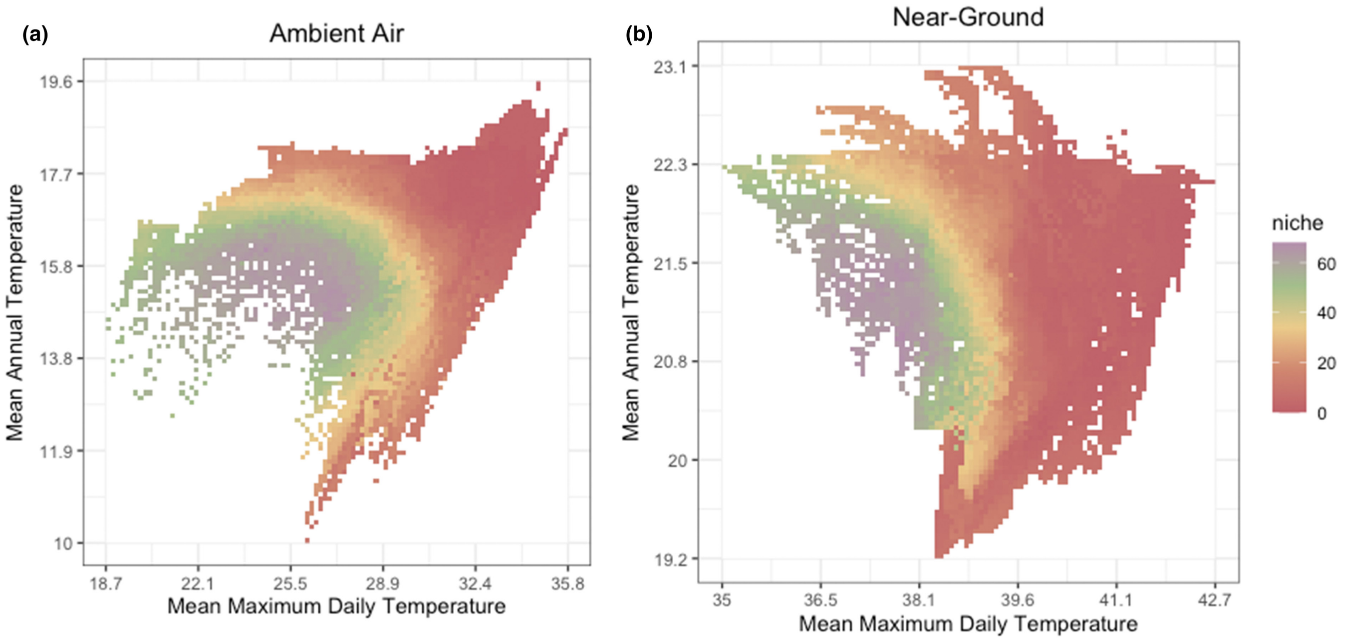

FIGURE 5 Visualizations of the temperature niche for the suite of species studied as species richness projections for 2009 to 2019

have had a greater impact on climate suitability for Fynbos species. We therefore propose that projections of climate change impacts would be more robust if the temperature data used to create SDMs reflected the conditions where these species live. By assuming an artificially inflated temperature gradient across geographical space, projections made using ambient air temperatures are likely to predict reduced climate change impact on species richness overall and misinterpret geographical patterns of change.

Our findings suggest that species richness projections made with ambient air temperatures may have underestimated the loss of suitable climate space most significantly along the northwest lowland plains and coastline, under both no dispersal and full dispersal scenarios. The northwest section of the biome, especially along the coastline, is an area with notable thermal divergence and particularly high maximum temperatures largely due to an offshore descending airstream. It is also the section of the biome where leaf temperatures near the ground have increased the fastest. Both types of hindcast projections suggest that western and central lowland coastal plains (<500 m elevation) are likely to have experienced high levels of species loss between the 1980s and the present day as a result of increasing temperatures. As opposed to poleward movement that typically characterizes climate change range shifts (Colwell et al., 2008; Lenoir & Svenning, 2015), species ranges have the potential to shift to lower latitudes, away from coastlines.

Due to suitable Fynbos climate space shifting inland, the ability of inland mountain regions to provide in- and ex-situ refugia (see: Ashcroft, 2010) – geographical regions that provide suitable climate conditions for long-term persistence during periods of environmental change – is likely to be of even greater importance in reducing climate change impacts on the plant and animal species that inhabit the Fynbos biome. In mountain locations, SDMs constructed using ambient air temperatures predicted marginally less species loss than SDMs constructed using near-ground leaf temperatures. However, SDMs constructed with ambient air temperatures did not predict the same degree or spread of potential climate suitability gain outside of our species' historical ranges. Thus, ambient air temperature SDMs potentially underestimate the potential for ex-situ refugia in these locations. In mountains, ambient air temperatures were found to be below the biome average, while near-ground leaf temperatures were close to their biome average, likely due to complex local weather patterns such as a reduced influence of onshore winds which warm coastal air temperatures. As a result, ambient air temperatures and near-ground leaf temperatures were particularly decoupled from one another in mountains, experiencing differences in mean daily mean temperature of up to 10°C. Consequently, projections derived from models constructed using ambient air temperatures could be underestimating the potential of higher elevation, inland sites to act as in- and ex-situ refugia under climate change, where principal floristic clades for Fynbos are presumed to have survived past climate changes (Linder, 2003; Verboom et al., 2014).

Accurate predictions of climate change impacts on species are required for future conservation management strategies. Many of the species inhabiting the Cape Floristic Region are endemics and are likely to be particularly at risk from climate change owing to their small geographic range sizes (Manes et al., 2021). Additionally, due to the hotspot's geographical placing on the poleward margin of the continent, species are unable to undergo significant range shifts poleward in response to warming (Trew & Maclean, 2021). Indeed, our study has demonstrated that a steep coastal climate gradient may be critically important in species' persistence in this particular hotspot and that – based on temperature change alone – Fynbos species are actually more likely to require dispersal routes to lower latitudes, into higher elevation areas away from the coastline. Unfortunately, many Fynbos species have limited dispersal capacity (Latimer et al., 2005), and the potential dispersal of lowland species to higher elevations is likely to be blocked by agricultural land (Guo et al., 2018); much of the Fynbos lowlands have already been converted and the remaining pockets are at high risk of future conversion (Altwegg et al., 2014). The near-ground species richness projections presented here demonstrate the importance of this gradient more clearly than projections created with ambient air temperatures, the latter projection type underestimating the losses and gains of suitable climate along the coastline.

Our findings should not be interpreted as faultless future predictions for the Fynbos Biome. Locations with suitable climate for a species may not become occupied, and so the results likely overestimate species richness overall. Additionally, we have constrained the species richness modelling to the Fynbos Biome for the computational efficiency of this study, and so the potential for species to exist outside of this area has not been included here. Moreover, temperature alone is not the sole determinant of species distribution, and variables more indicative of water availability – such as soil moisture – would be needed in order to accurately forecast the distributions of species, especially in this biome where water availability, fire occurrence, and soil types are important limiting factors for Fynbos species (Ackerly et al., 2014; Altwegg et al., 2014). Nevertheless, temperature is considered a key driver of biological processes in the Fynbos biome (Altwegg et al., 2014), and field studies have shown that some species in the succulent karoo (a shrublands biome bordering the xeric inland extremes of the Fynbos biome) are already living close to their temperature limit (Altwegg et al., 2014). Additionally, the primary cause of the divergence between ambient air and near-ground leaf temperatures, namely solar radiation, is likely to result in differences between soil moisture estimates, as solar radiation is a key determinant of evapotranspiration (Campbell & Norman, 2012). As our goal was to clearly understand the effect of spatial variance in leaf temperatures on SDMs, we did not include variables relating to water availability or soil type in the construction of the models. Instead, our study reveals how the use and influence of ambient air temperature in a more comprehensive set of environmental variables could undermine an SDM and suggests that ambient air temperatures may be an ineffective surrogate for predicting the impact of climate change on species that live near the near ground. Our results are very similar to findings by Lembrechts et al. (2019) and Storlie et al. (2014) in forest environments, despite the different environmental system used here, and thus confirms the importance of microclimatic processes in SDM predictions. Finding new ways of incorporating near-ground environmental variables into assessments of species' vulnerability to climate change is an important avenue for future work.

Despite the heavy reliance on species distribution models to forecast species responses to future climate changes, such models are rarely constructed using climate data indicative of the conditions organisms experience. Our findings suggest that ambient air temperatures may be a poor surrogate for near-ground temperatures, yet a significant proportion of plant and animal species live near the ground; especially in biodiversity-rich Mediterranean-type systems. We have demonstrated that spatial gradients in temperatures in the Fynbos Biome are likely to be significantly reduced using near the ground leaf temperatures, and further investigations are required in other Mediterranean-type systems. In consequence, SDMs constructed using ambient air temperatures are likely to predict an artificially broad thermal niche for ground-dwelling species. Near-ground leaf temperature data have typically been unavailable at regional scales. However, recent methodological development in the field of microclimatology, as well as the recent *SoilTemp* database release (see: Lembrechts et al., 2020), makes modelling of temperature conditions experienced by organisms possible, without the need to deploy temperature loggers (e.g. Bennie et al., 2013; Maclean, 2019; Maclean et al., 2017 . As demonstrated in this study, it is now possible to model leaf temperatures at specified heights above the ground, in any geographical location, and use these variables to forecast species responses to warming. These methodological advances are important in our understanding of climate change impacts on biodiversity and therefore help increase the effectiveness of conservation strategies designed to mitigate potential negative effects. In the case of the Fynbos Biome and other Mediterranean-type ecosystems, they can help further to develop the existing forecasts to aid conservation planning for these regions.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13540.

DATA AVAILABILITY STATEMENT

All datasets used are third-party datasets available freely on public repositories. The occurrence data for plant species in the Cape floristic Region are freely available from the Global Biodiversity Information Facility (www.gbif.org), and the occurrence data used in this study is available at: https://doi.org/10.5281/zenodo.6374097; the hourly climate data are available from the ERA5 fifth-generation ECMWF atmospheric reanalysis of the global climate (https://cds.climate.copernicus.eu/cdsapp#!/home); hourly near-ground temperatures are fully reproducible using the microclimf package for R 4.0 (https://mrke.github.io); temperature data from the Cederberg used for verification were sourced via the SOILTEMP global database of soil temperatures (https://soiltemp.weebly.com/). All figures created for this study are also available on Figshare (private link: https://figshare.com/s/d40f9cb44441b252318c).

ORCID

Brittany T. Trew https://orcid.org/0000-0002-0649-828X

REFERENCES

Aalto, J., Scherrer, D., Lenoir, J., Guisan, A., & Luoto, M. (2018). Biogeophysical controls on soil-atmosphere thermal differences: implications on warming Arctic ecosystems. *Environmental Research Letters*, *13*(7), 074003. https://doi.org/10.1088/1748-9326/aac83e

Ackerly, D. D., Stock, W. D., & Slingsby, J. A. (2014). Geography, climate, and biodiversity: The history and future of mediterranean-type ecosystems. In N. Allsopp, J. F. Colville, & G. A. Verboom (Eds.), *Fynbos: Ecology, evolution, and conservation of a megadiverse region* (pp. 361–375). Oxford University Press.

Allsopp, N., Colville, J. F., Verboom, G. A., & Cowling, R. M. (2014). *Fynbos: Ecology, evolution, and conservation of a megadiverse region*. Oxford University Press.

Altwegg, R., West, A., Gillson, L., & Midgley, G. F. (2014). Impacts of climate change in the Greater Cape Floristic Region. In N. Allsopp, J. F. Colville, & G. A. Verboom (Eds.), *Fynbos: Ecology, evolution, and conservation of a megadiverse region* (pp. 299–320). Oxford University Press.

Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*(10), 1677–1688. https://doi.org/10.1111/j.1365-2699.2006.01584.x

Ashcroft, M. B. (2010). Identifying refugia from climate change. *Journal of Biogeography*, *37*, 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x

Barry, R. G., & Blanken, P. D. (2016). *Microclimate and local climate*. Cambride University Press.

Bennie, J., Hodgson, J. A., Lawson, C. R., Holloway, C. T. R., Roy, D. B., Brereton, T., Thomas, C. D., & Wilson, R. J. (2013). Range expansion through fragmented landscapes under a variable climate. *Ecology Letters*, *16*(7), 921–929. https://doi.org/10.1111/ele.12129

Bergh, N. G., Verboom, G. A., Rouget, M., & Cowling, R. M. (2014). Vegetation types of the greater cape floristic region. In N. Allsopp, J. F. Colville, & G. A. Verboom (Eds.), *Fynbos: ecology, evolution, and conservation of a megadiverse region* (pp. 1–25). Oxford University Press.

Boyce, M. S., Vernier, P. R., Nielsen, S. E., & Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecological Modelling*, *157*, 281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Bradshaw, P. L., & Cowling, R. M. (2014). Landscapes, rock types, and climate of the Greater Cape Floristic Region. In N. Allsopp, J. F. Colville, & G. A. Verboom (Eds.), *Fynbos: ecology, evolution, and conservation of a megadiverse region* (pp. 26–42). Oxford University Press.

Bramer, I., Anderson, B. J., Bennie, J., Bladon, A. J., De Frenne, P., Hemming, D., Hill, R. A., Kearney, M. R., Körner, C., Korstjens, A. H., Lenoir, J., Maclean, I. M. D., Marsh, C. D., Morecroft, M. D., Ohlemüller, R., Slater, H. D., Suggitt, A. J., Zellweger, F., & Gillingham, P. K. (2018). *Advances in monitoring and modelling climate at ecologically relevant scales* (pp. 101–161). Elsevier.

Braschler, B., Duffy, G. A., Nortje, E., Kritzinger-Klopper, S., Du Plessis, D., Karenyi, N., Leihy, R. I., & Chown, S. L. (2020). Realised rather than fundamental thermal niches predict site occupancy: Implications for climate change forecasting. *Journal of Animal Ecology*, *89*, 2863–2875. https://doi.org/10.1111/1365-2656.13358

Breiman, L., Friedman, J. H., Olshen, R. A., & Stone, C. J. (1984). *Classification and regression trees* (1st ed.). Routledge. https://doi.org/10.1201/9781315139470

Broennimann, O., Di Cola, V., & Guisan, A. (2020). ecospat: spatial ecology miscellaneous methods. R package version 3.1. https://CRAN.Rproject.org/package=ecospat

Campbell, G. S. (1986). Extinction coefficients for radiation in plant canopies calculated using an ellipsoidal inclination angle distribution. *Agricultural and Forest Meteorology*, *36*, 317–321. https://doi.org/10.1016/0168-1923(86)90010-9

Campbell, G. S., & Norman, J. M. (2012). *An introduction to environmental biophysics* (2nd ed.). Springer Science+Business Media.

Colwell, R. K., Brehm, G., Cardelús, C. L., Gilman, A. C., & Longino, J. T. (2008). Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, *322*(5899), 258–261. https://doi.org/10.1126/science.1162547

Copernicus Climate Change Service (C3S). (2017). ERA5: Fifth generation of ECMWF atmospheric reanalyses of the global climate. Copernicus Climate Change Service Climate Data Store. https://cds.climate.copernicus.eu/cdsapp#!/home

Di Cola, V., Broennimann, O., Petitpierre, B., Breiner, F. T., D'Amen, M., Randin, C., Engler, R., Pottier, J., Pio, D., Dubuis, A., Pellissier, L., Mateo, R. G., Hordijk, W., Salamin, N., & Guisan, A. (2017). ecospat: an R package to support spatial analyses and modeling of species niches and distributions. *Ecography*, *40*, 774–787. https://doi.org/10.1111/ecog.02671

Elith, J., & Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159

Ferrier, S., & Guisan, A. (2006). Spatial modelling of biodiversity at the community level. *Journal of Applied Ecology*, *43*(3), 393–404. https://doi.org/10.1111/j.1365-2664.2006.01149.x

Greenwell, B., Boehmke, B., Cunningham, J., & Developers, G. B. M. (2020). gbm: Generalized Boosted Regression Models. R package version 2.1.8. https://CRAN.R-project.org/package=gbm

Guisan, A., & Thuiller, W. (2005). Predicting species distribution: offering more than simple habitat models. *Ecology Letters*, *8*(9), 993–1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guo, F., Lenoir, J., & Bonebrake, T. C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, *9*, 1315. https://doi.org/10.1038/s41467-018-03786-9

Kearney, M., & Porter, W. P. (2004). Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology*, *85*(11), 3119–3131. https://doi.org/10.1890/03-0820

Kearney, M., & Porter, W. (2009). Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters*, *12*(4), 334–350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Kelliher, F. M., Leuning, R., Raupach, M. R., & Schulze, E. D. (1995). Maximum conductances for evaporation from global vegetation types. *Agricultural and Forest Meteorology*, *73*, 1–16. https://doi.org/10.1016/0168-1923(94)02178-M

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, *21*, 393–404. https://doi.org/10.1111/j.1466-8238.2011.00686.x

Körner, C., & Hiltbrunner, E. (2018). The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics*, *30*, 16–21. https://doi.org/10.1016/j.ppees.2017.04.004

Latimer, A. M., Silander, J. A., & Cowling, R. M. (2005). Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science*, *309*, 1722–1725. https://doi.org/10.1126/science.1115576

Lembrechts, J. J., Aalto, J., Ashcroft, M. B., De Frenne, P., Kopecký, M., Lenoir, J., Luoto, M., Maclean, I. M. D., Roupsard, O., Fuentes-Lillo, E., García, R. A., Pellissier, L., Pitteloud, C., Alatalo, J. M., Smith, S. W., Björk, R. G., Muffler, L., Ratier Backes, A., Cesarz, S., … Nijs, I. (2020). SoilTemp: a global database of near-surface temperature. *Global Change Biology*, *26*(11), 6616–6629. https://doi.org/10.1111/gcb.15123

Lembrechts, J. J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider, S., Pellissier, L., Pauchard, A., Ratier Backes, A., Dimarco, R. D., Nuñez, M. A., Aalto, J., & Nijs, I. (2019). Comparing temperature data sources for use in species distribution models: From in-situ logging to remote sensing. *Global Ecology and Biogeography*, *28*(11), 1578–1596. https://doi.org/10.1111/geb.12974

Lembrechts, J. J., Nijs, I., & Lenoir, J. (2018). Incorporating microclimate into species distribution models. *Ecography*, *42*(7), 1267–1279. https://doi.org/10.1111/ecog.03947

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology & Evolution*, *4*, 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Lenoir, J., Hattab, T., & Pierre, G. (2017). Climatic microrefugia under anthropogenic climate change: implications for species redistribution. *Ecography*, *40*, 253–266. https://doi.org/10.1111/ecog.02788

Lenoir, J., & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography*, *38*, 15–28. https://doi.org/10.1111/ecog.00967

Linder, H. P. (2003). The radiation of the Cape flora, southern Africa. *Biological Reviews*, *78*, 597–638. https://doi.org/10.1017/S1464793103006171

Macalister, D., Muasya, A. M., Crespo, O., Ogola, J. B. O., Maseko, S. T., Valentine, A. J., Ottosen, C.-O., Rosenqvist, E., & Chimphango, S. B. M. (2020). Effect of temperature on plant growth and stress tolerant traits in rooibos in the Western Cape, South Africa. *Scientia Horticulturae*, *263*, 109137. https://doi.org/10.1016/j.scienta.2019.109137

Maclean. (2022). *microclimf: Fast above, below or within canopy gridded microclimate modelling with R*. https://github.com/ilyamaclean

Maclean, I. M. D., Duffy, J. P., Haesen, S., Govaert, S., De Frenne, P., Vanneste, T., Lenoir, J., Lembrechts, J. J., Rhodes, M. W., & Van Meerbeek, K. (2021). On the measurement of microclimate. *Methods in Ecology and Evolution*, *12*(8), 1397–1410. https://doi.org/10.1111/2041-210X.13627

Maclean, I. M. D., & Klinges, D. H. (2021). Microclimc: A mechanistic model of above, below and within-canopy microclimate. *Ecological Modelling*, *451*, 109567. https://doi.org/10.1016/j.ecolmodel.2021.109567

Maclean, I. M. D., Mosedale, J. R., & Bennie, J. J. (2019). Microclima: An r package for modelling meso- and microclimate. *Methods in Ecology and Evolution*, *10*, 280–290.

Maclean, I. M. D. (2019). Predicting future climate at high spatial and temporal resolution. *Global Change Biology 26*, 1003–1011.

Maclean, I. M. D., Suggitt, A. J., Wilson, R. J., Duffy, J. P., & Bennie, J. J. (2017). Fine-scale climate change: modelling spatial variation in biologically meaningful rates of warming. *Global Change Biology*, *23*, 256–268. https://doi.org/10.1111/gcb.13343

Manes, S., Costello, M. J., Beckett, H., Debnath, A., Devenish-Nelson, E., Grey, K.-A., Jenkins, R., Khan, T. M., Kiessling, W., Krause, C., Maharaj, S. S., Midgley, G. F., Price, J., Talukdar, G., & Vale, M. M. (2021). Endemism increases species' climate change risk in areas of global biodiversity importance. *Biological Conservation*, *257*, 109070. https://doi.org/10.1016/j.biocon.2021.109070

McCullagh, P., & Nelder, J. A. (1983). *Generalized linear models* (2nd ed.). Routledge. https://doi.org/10.1201/9780203753736

Michaletz, S. T., Weiser, M. D., Zhou, J., Kaspari, M., Helliker, B. R., & Enquist, B. J. (2015). Plant thermoregulation: Energetics, trait–environment interactions, and carbon economics. *Trends in Ecology & Evolution*, *30*(12), 714–724. https://doi.org/10.1016/j.tree.2015.09.006

Midgley, G. F., Hannah, L., Millar, D., Rutherford, M. C., & Powrie, L. W. (2002). Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. *Global Ecology and Biogeography*, *11*, 445–451. https://doi.org/10.1046/j.1466-822X.2002.00307.x

Midgley, G. F., Hannah, L., Millar, D., Thuiller, W., & Booth, A. (2003). Developing regional and species-level assessments of climate change impacts on biodiversity in the Cape Floristic Region. *Biological Conservation*, *112*, 87–97. https://doi.org/10.1016/S0006-3207(02)00414-7

Monteith, J., & Unsworth, M. (2013). *Principles of environmental physics: Plants, animals, and the atmosphere*. Academic Press.

Naimi, B., & Araújo, M. B. (2016). sdm: A reproducible and extensible R platform for species distribution modelling. *Ecography*, *39*, 368–375. https://doi.org/10.1111/ecog.01881

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

R Core Team (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Raupach, M. R. (1994). Simplified expressions for vegetation roughness length and zero-plane displacement as functions of canopy height and area index. *Boundary-Layer Meteorology*, *71*, 211–216. https://doi.org/10.1007/BF00709229

Ripley, B. D. (1996). *Pattern recognition and neural networks*. Cambridge University Press.

Rundel, P. W., Arroyo, M. T. K., Cowling, R. M., Keeley, J. E., Lamont, B. B., & Vargas, P. (2016). Mediterranean biomes: Evolution of their vegetation, floras, and climate. *Annual Review of Ecology, Evolution, and Systematics*, *47*, 383–407. https://doi.org/10.1146/annurev-ecolsys-121415-032330

Ryan, B. C. (1977). A Mathematical model for diagnosis and prediction of surface winds in mountainous terrain. *Journal of Applied Meteorology and Climatology*, *16*, 571–584. https://doi.org/10.1175/1520-0450(1977)016<0571:AMMFDA>2.0.CO;2

Santini, L., Benítez-López, A., Maiorano, L., Čengić, M., & Huijbregts, M. A. J. (2021). Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions*, *27*(6), 1035–1050. https://doi.org/10.1111/ddi.13252

Sarmento Cabral, J., Jeltsch, F., Thuiller, W., Higgins, S., Midgley, G. F., Rebelo, A. G., Rouget, M., & Schurr, F. M. (2013). Impacts of past habitat loss and future climate change on the range dynamics of South African Proteaceae. *Diversity and Distributions*, *19*, 363–376. https://doi.org/10.1111/ddi.12011

South African National Biodiversity Institute. (2018). The Vegetation Map of South Africa, Lesotho and Swaziland. In L. Mucina, M. C. Rutherford, & L. W. Powrie (Eds.), Online, http://bgis.sanbi.org/Projects/Detail/186, Version 2018

Specht, R. L., & Moll, E. J. (1983). Mediterranean-type heathlands and Sclerophyllous Shrublands of the world: An overview. In F. J. Kruger, D. T. Mitchell, & J. U. M. Jarvis (Eds.), *Mediterranean-Type Ecosystems. Ecological Studies*, vol *43*. Springer. https://doi.org/10.1007/978-3-642-68935-2_2

Storlie, C., Merino-Viteri, A., Phillips, B., Vanderwal, J., Welbergen, J., & Williams, S. (2014). Stepping inside the niche: microclimate data are critical for accurate assessment of species' vulnerability to climate change. *Biology Letters*, *10*, 20140576. https://doi.org/10.1098/rsbl.2014.0576

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., De Siqueira, M. F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., Van Jaarsveld, A. S., Midgley, G. F., Miles, L., Ortega-Huerta, M. A., Townsend Peterson, A., Phillips, O. L., & Williams, S. E. (2004). Extinction risk from climate change. *Nature*, *427*, 145–148. https://doi.org/10.1038/nature02121

Thuiller, W., Georges, D., Engler, R., Breiner, F., Georges, M. D., & Thuiller, C. W. (2016). Package 'biomod2'. ftp://ftp2.de.freebsd.org/pub/misc/cran/web/packages/biomod2/biomod2.pdf

Tingley, M. W., & Beissinger, S. R. (2013). Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology*, *94*(3), 598–609. https://doi.org/10.1890/12-0928.1

Trew, B. T., & Maclean, I. M. D. (2021). Vulnerability of global biodiversity hotspots to climate change. *Global Ecology and Biogeography*, *30*(4), 768–783. https://doi.org/10.1111/geb.13272

Verboom, G. A., Linder, H. P., Forest, F., Hoffmann, V., Bergh, N. G., & Cowling, R. M. (2014). Cenozoic assembly of the greater cape flora. In N. Allsopp, J. F. Colville, & G. A. Verboom (Eds.), *Fynbos: Ecology, evolution and conservation of a megadiverse region* (pp. 93–118). Oxford University Press.

BIOSKETCH

The authors are interested in how ecological and biogeographical research can improve the forecasts of global biodiversity's vulnerability to climate change and their application in conservation. They work with a multitude of ecosystems, taxa, and geographic regions, using both field and computational studies.

Author contributions: B.T.T. and I.M.D.M. designed the research; B.T.T. and J.P.D. performed the climate modelling; B.T.T. performed the species distribution modelling and analysed results; S.L.C. provided temperature logger data for model validation; B.T.T. wrote the manuscript with contributions from I.M.D.M., R.E., J.P.D., and S.L.C.

SUPPORTING INFORMATION

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