

Full title: Species distribution modelling of three *Acacia* species in the Negev Desert: predicting future range shifts and identifying climatic drivers

Short title: Species distribution Model of Acacia trees

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Abstract

Climate change is intensifying aridity across desert regions, causing ecological stress and threatening the stability of arid ecosystems. As keystone species are central to ecosystem functioning, predicting shifts in their distribution can provide important insight into broader ecological change. In the Negev Desert, *Acacia* populations have experienced widespread declines attributed to reduced surface water availability. However, their future persistence remains uncertain due to poorly defined survival thresholds and variability in climate projections. This study applies Species Distribution Modelling (SDM) using MaxEnt to estimate present and future habitat suitability of the three *Acacia* species in the Negev, *Acacia tortilis*, *Acacia raddiana* and *Acacia pachyceras*, across multiple emission scenarios. Results indicate that suitable habitat for

all species may initially expand westwards under mid-century or low-emission scenarios, but contract under higher-emission scenarios later in the century resulting in overall habitat loss. Model outcomes were sensitive to the geographic extent used for model calibration, with broader extents overestimating suitability predictions by failing to capture the local ecological context. Environmental drivers of species' distributions were assessed using SDMs alongside climatic niche analysis. *A. tortilis* is a thermophilic specialist restricted to hotter environments, *A. raddiana* shows broad tolerance across climatic gradients, and the narrow distribution of *A. pachyceras* appears driven primarily by water availability. Notably, results revealed significant climatic niche similarity between *A. tortilis* and *A. pachyceras* despite having non-overlapping geographic ranges, suggesting that non-climatic factors may influence their realised distributions. This study identifies key considerations for improving future predictions of *Acacia* distributions in the Negev.

1. Introduction

Acacia species are highly adapted to arid environments and inhabit many desert regions globally (Uni et al., 2022)¹. In the Negev Desert, they act as keystone species, providing essential habitat, shade and food resources for many desert organisms and improving soil fertility through nitrogen fixation (Wiegand et al., 1999)². Therefore, changes in *Acacia* population size and distribution will have significant implications for ecosystem functioning and biodiversity. Three *Acacia* taxa inhabit the Negev: *A. raddiana* (Savi), *A. tortilis* (Forssk.), and *A. pachyceras* (*O. Schwartz*; formerly *gerrardii* [Benth.] or *negevensis* [Zohary]) (Stavi et al., 2014)³. Their distributions are strongly influenced by spatial variation in climate across the region.

The Negev Desert spans multiple climate zones over a relatively short distance, transitioning from the semi-arid north to the hyper-arid south. Within this range, the elevated Negev Highlands are comparatively cooler and wetter, contrasting with the low-lying, hyper-arid Arava Valley which runs along the eastern border with Jordan (Figure 1) (Portnov and Safriel, 2004⁽⁴⁾; Collins-Kreiner and Wall, 2007⁽⁵⁾). The Negev forms the southern, arid end of an even steeper bioclimatic gradient across the Israel-Palestine region, with pronounced latitudinal variation in precipitation, temperature and topography (Prince and Jackson, 2020)⁶. This steep environmental gradient makes the region an ideal study area for examining the climatic controls on *Acacia* species distributions.

Figure 1. a) Climatic zones across Israel-Palestine demonstrating the north-south aridity gradient (modified from Portnov and Safriel, 2004)⁴. **b)** Map of the Negev desert and its subregions, featuring the Negev Highlands and the Arava Valley (modified from Collins-Kreiner and Wall., 2007)⁵

Acacia raddiana and *A. tortilis* in the Middle East are classified as Sudanian elements originating from the Sudanian phytogeographic region of Africa that expanded northward into the Saharo-Arabian desert (Danin, 1992)⁷. In the Negev, these species occur at the northern edge of their range and persist under very different ecological conditions compared to the East African savannas (Shmida and Aronson, 1986)⁸. Although *A. pachycera* is native to the Middle East and Arabian peninsula (Suleiman et al. 2017)⁹, the Negev desert also represents the northern limit of its natural distribution. Differences in climatic regime and community composition suggest that Negev populations occupy an environmentally distinct portion of the species' broader realised niche. Consequently, the *Acacia* populations of the Negev should be examined within the distinct environmental context of this desert system.

Identifying tree species that are capable of surviving under extreme conditions is increasingly important as climate stress intensifies in dryland ecosystems. Acacia trees demonstrate strong drought tolerance through their ability to continue photosynthesis during peak summer, unlike many desert plants that become dormant during hot, dry seasons to conserve water (Uni et al., 2022)¹. However, despite their resilience to prolonged drought, acacias still require periodic hydrological recharge above a minimum, yet unknown, threshold (Winters et al., 2018)¹⁰. Water supply is largely determined by episodic precipitation events, with a single flash flood able to recharge subsurface moisture reserves sufficiently to sustain adult trees for many years (Babad et al., 2024)¹¹. Hydrological conditions are especially critical during early stages of the acacia life cycle as successful seedling establishment depends on moisture availability from winter flooding, and prolonged drought following germination drought creates a high risk of seedling mortality (Wiegand et al., 1999)². Projected decreases in mean rainfall (Peleg et al., 2015)¹², combined with uncertainty in precipitation timing and intensity, raise serious concerns about whether recruitment thresholds will be met in the future. Exceeding critical aridity thresholds can trigger abrupt ecological transitions, accelerating desertification and habitat loss (Berdugo et al., 2021)¹³.

Evidence suggests that recent conditions may already be failing to meet this hydrological requirement. Significant declines have been documented across the Negev in recent decades (Stavi et al., 2015)¹⁴, attributed to reductions in surface and subsurface water availability caused by both anthropogenic disturbances and climate change (Armoza-Zvuloni et al., 2021⁽¹⁵⁾; Isaacson et al., 2023⁽¹⁶⁾). Regional climatic drying and decreasing precipitation have been identified as primary drivers of *Acacia* decline, particularly in the southern Negev where warming and drying are most intense (Stavi et al., 2014⁽³⁾; Isaacson et al., 2023⁽¹⁶⁾). Anthropogenic disturbances that alter surface water flow, such as roads and dam construction, have also been associated with increased mortality

and reduced recruitment by disrupting flood-driven recharge processes (Ward and Rohner, 1997)¹⁷.

Acacia populations also face various biotic pressures, including parasitic plants, bruchid beetle infestation and the decline of mammalian herbivores for seed dispersal (Or and Ward, 2003)¹⁸. However, most studies conclude that reduced surface water availability remains the dominant driver of widespread decline observed in recent decades (Stavi et al., 2014⁽³⁾; Shrestha et al., 2003⁽¹⁹⁾).

In addition to climatic conditions, edaphic and landscape features mediate water availability for acacia trees, as soil characteristics and landscape position influence infiltration, drainage, water retention and loss (Patten and Ellis, 1995)²⁰. Due to the low rainfall in the Negev, acacia trees are largely restricted to ephemeral stream beds (wadis), where soil moisture is higher than surrounding slopes due to the concentration of runoff (Isaacson et al., 2023⁽¹⁶⁾, Babad et al., 2024⁽¹¹⁾).

The three Negev *Acacia* taxa have distinct ecological characteristics. *A. raddiana* and *A. tortilis* are prevalent throughout the region and are considered keystone species (Uni et al., 2021)²¹. *A. tortilis* is typically associated with hotter, drier environments, particularly the Arava Valley, demonstrating higher water-use efficiency under low soil moisture conditions which allows it to persist in areas where water pulses are infrequent (Uni et al., 2023b)²². *A. raddiana* is the most widespread, occupying a much broader climatic range and overlapping in distribution with both other species (Wiegand et al., 1999)². It is commonly found within main channels where soil moisture is more stable (Uni et al., 2023b)²². *A. pachyceras* has a more restricted distribution, occurring primarily in the Negev Highlands at cooler temperatures, and does not overlap with *A. tortilis* which occupies comparatively hotter environments.

While previous research has examined the physiological and hydrological mechanisms of Negev acacias, substantial uncertainty remains regarding their ecological thresholds and future responses to climate change. In particular, it is unclear whether increasing aridity will favour these desert-adapted species by expanding suitable desert habitat, or instead push populations beyond their ecological tolerances and drive further decline. These responses are likely to differ between species and across future climate scenarios.

Species Distribution Modelling (SDM) provides a useful framework for exploring these potential responses. SDMs estimate a species' suitable habitat by relating known species occurrence records to environmental variables and projecting these relationships onto future climate scenarios to estimate potential range shifts (Warren and Seifert, 2011)²³. The MaxEnt algorithm is a widely used SDM approach for presence-only data, estimating suitability by contrasting environmental conditions at occurrence locations with those at randomly sampled background points (Phillips et al., 2006)²⁴.

SDMs help identify the environmental drivers influencing species distributions, providing initial insight into the factors that shape their ecological niche. To deepen the analysis of species' ecological niches beyond distribution patterns, Warren et al. (2008)²⁵ introduced statistical frameworks that quantify niche overlap between species and test the significance of these patterns. Climatic niche overlap analysis is widely used to assess the degree of similarity or divergence between the ecological niches of closely related taxa, rather than inferring this from geographic distributions alone (Warren et al., 2008⁽²⁵⁾; Zhao et al., 2019⁽²⁶⁾). Since climatic niches do not always align with geographic distributions (Cardillo and Warren, 2016)²⁷, it is useful to quantify this statistically.

A commonly applied framework for quantifying climatic niche overlap is the ‘PCA-env’ method developed by Broennimann et al. (2012)²⁸. Principal Component Analysis (PCA) summarises predictors into a reduced set of orthogonal axes representing the main gradients of environmental variation, allowing species’ niches to be compared within a shared environmental space (Zhao et al., 2019). Niche overlap between species is quantified using the Schoener’s D metric, ranging from 0 (no overlap) to 1 (complete overlap), providing a standardised measure of similarity in environmental space. Subsequently, the significance of these observed overlap values are determined by two statistical tests (Warren et al., 2008)²⁵. The niche equivalency test evaluates whether two species occupy identical niches, while the niche similarity test assesses whether niches are more similar than expected given the environmental background available to each species (Xian et al., 2023)²⁹.

These approaches have not yet been applied to acacias in the Negev, yet they can offer essential insight for anticipating the long-term responses of these keystone species to future climate change, with important implications for wider ecological change across the Negev.

To strengthen the robustness of future predictions, it is also important to critically evaluate the modelling framework itself. Given that SDMs characterise species-environment relationships relative to the environmental background, model outcomes are highly sensitive to the spatial extent used to define that background (Vale et al., 2013)³⁰. Calibrating models using local extents has been shown to better reflect real distributions because they capture region-specific environmental relationships (Anselmetto et al., 2024)³¹. However, this can result in niche truncation where only a portion of the species’ niche is represented, potentially reducing predictive accuracy under novel future climates (Guisan et al., 2025)³². Models calibrated across broader extents are more likely to capture the species’ full climatic range, but they tend to overgeneralise predictions because

species-environment relationships vary across geographic contexts (McPherson and Jetz, 2007)³³. Thus, there is a trade-off between representing the broader climatic envelope and maintaining regional ecological relevance. This study therefore considers multiple calibration extents to provide more comprehensive and robust projections of future species distributions.

Overall, this study investigates the present and future distributions of *A. raddiana*, *A. tortilis*, and *A. pachyceras* in the Negev Desert under a range of climate scenarios. SDMs and climatic niche analyses are used to identify the environmental drivers that shape species ecological niches and their distributions. Understanding the roles of these factors in determining Acacia niches will enable us to evaluate model predictions of current- and future species distribution. An evaluation of calibration extent as a key modelling parameter should also improve the robustness of present- and future predictions. The goal of this study is thus to answer the three following research questions (RQs):

1. What are the key environmental factors shaping the distributions and niche characteristics of the three *Acacia* species?
2. How might the distributions of the three *Acacia* species shift under future climate change?
3. How does the study area extent influence model outputs?

2. Methods

2.1 Study Area

The study extent across Israel-Palestine was delineated to capture the north-south aridity gradient of the Negev within its broader regional context. To align with the spatial coverage of available occurrence data, the study area was constrained to national administrative boundaries (Level 0) for Israel and Palestine obtained from the Global Administrative Areas database (GADM v4.1) via the geodata R package (Hijmans et al., 2025)³⁴.

2.2 Species Occurrence Data

Occurrence data for *A. tortilis* and *A. raddiana* were downloaded from the Global Biodiversity Information Facility (GBIF.org, 2025a⁽³⁵⁾; 2025b⁽³⁶⁾). GBIF lacks a complete or reliable dataset for *A. pachyceras* due to its unresolved taxonomic classification and data scarcity in remote regions (Suleiman et al., 2017⁽⁹⁾; Chanachai et al., 2024⁽³⁷⁾). Therefore, a localised national dataset for *A. pachyceras* was provided by the Acacia Research Centre, Dead Sea and Arava Science Centre (DSASC) (Groner, 2025)³⁸. Occurrence records were cleaned to remove incomplete or duplicate records, then spatially thinned using a minimum distance threshold of 100m, corresponding to the resolution of the environmental predictors in order to reduce sampling bias while retaining as much data as possible (Castellanos et al., 2019³⁹; Kim et al., 2025⁴⁰). After thinning, 1045 spatially independent occurrence records remained for *A. tortilis*, and 2171 for *A. raddiana*. Thinning was not applied to *A. pachyceras* because the sample size was already small (134 records), and thinning may reduce model performance where occurrence data are sparse (Ten Caten and Dallas, 2023)⁴¹.

Figure 2. Study area with occurrence points of *Acacia tortilis*, *A. raddiana*, and *A. pachyceras*. Inset map shows position within the Middle East.

2.3 Environmental Data

Climate data were obtained from the CHELSA bioclimatic dataset (Karger et al., 2017)⁴², selected because it accounts for terrain-driven and orographic processes which improve climatic representation in regions with complex topography and sparse meteorological coverage such as the Negev Desert (Karger et al., 2017⁴²; Prince and Jackson, 2020⁶). All 19 standard bioclimatic variables were downloaded for initial analysis at a spatial resolution of 30 arc-second (~1 km).

Bioclimatic variables were selected based on their ecological relevance to *Acacia* species; highly correlated predictors ($| \text{Pearson's } r | \geq 0.8$) were excluded. BIO12 (Annual Precipitation) was selected as it represents long-term water input to the system, influencing soil moisture availability and species' survival thresholds (Behroozian et al., 2025)⁴³. BIO15 (Precipitation Seasonality) captures how rainfall is distributed throughout the year, reflecting the ecological importance of rainfall variability and pulse dynamics for germination, growth, and seedling establishment (Babad et al., 2024)¹¹. BIO5 (Maximum Temperature of the Warmest Month) was selected to represent upper thermal limits, while BIO11 (Mean Temperature of the Coldest Quarter) captures lower thermal constraints. BIO2 (Mean Diurnal Range) was retained as it did not exhibit high collinearity and also captures an additional dimension of climatic variability.

To better represent fine-scale environmental variation, particularly for *A. pachyceras* which occupies a smaller geographic area, climatic layers were resampled from 1km to 100m resolution using bilinear interpolation. Importantly, resampling did not add new information: it only redfined

the structure by subdividing grid cells, allowing environmental gradients to be represented at a finer scale.

Variables representing the local terrain were considered to capture fine-scale controls that are not represented by climatic predictors. Although topography was initially considered, elevation was found to be strongly correlated with temperature-related variables due to the altitudinal control on temperature (Shanan et al., 1967)⁴⁴. As temperature is a more direct driver of *Acacia* physiological limits, climatic predictors were prioritized.

Terrain influences at the local scale were captured through proximity to ephemeral stream channels. A high-resolution stream network was constructed by integrating official drainage line data from the Jewish National Fund (Hebrew University of Jerusalem GIS Centre, 2025)⁴⁵ with OpenStreetMap waterway vectors (OSM contributors, 2025)⁴⁶ to capture smaller tributaries. This was then rasterised and converted to a Euclidean distance surface using the GDAL Proximity algorithm.

Soil texture (sand and clay content) and bulk density are relevant predictors as they influence water-holding capacity and infiltration (Dung et al., 2020)⁴⁷. These variables were obtained from the SoilGrids database (Poggio et al., 2021)⁴⁸ using the geodata R package (Hijmans, 2025)³⁴, and a composite 0–30 cm layer was created by averaging values from the 0–5, 5–15, and 15–30 cm depth intervals. This represents the biologically active upper soil profile which is the primary interface for water infiltration and the most critical zone for seedling establishment (Wiegand et al., 1999)².

SoilGrids layers, provided at 30 arc-second (~1 km) resolution, were resampled to 100m to match the spatial resolution of the environmental predictors. Isolated missing data cells in soil rasters

were infilled using GDAL’s Inverse Distance Weighting (IDW) algorithm with a 100-pixel search radius, a robust method for interpolating continuous soil surfaces (Igaz et al., 2021)⁴⁹. These soil properties were held constant for future projections as they typically change over much longer time scales and are therefore commonly treated as static in SDMs (Zangiabadi et al., 2021)⁵⁰. After preliminary model runs, clay content was excluded as a predictor due to its negligible contribution. The final predictor set is summarised in Table 1.

Table 1. Final environmental variables used in this study

Category	Variable
Bioclimatic	BIO2 (Mean Diurnal Range) (°C)
	BIO5 (Maximum Temperature of Warmest Month (°C)
	BIO11 (Mean Temperature of Coldest Quarter) (°C)
	BIO12 (Annual Precipitation) (mm)
	BIO15 (Precipitation Seasonality) (%)
Edaphic	Sand Content (%)
	Bulk Density (g/cm ³)
Hydrological	Distance to Streams (m)

2.4 Species Distribution Modelling

MaxEnt model outputs represent relative habitat suitability on a continuous scale from 0–1 for each grid cell (Elith et al., 2010)⁵¹. Model performance was evaluated using the Area Under the Receiver Operating Characteristic Curve (AUC) which measures the model’s ability to

discriminate between presence locations and background conditions (Elith et al., 2010)⁵¹, with values closer to 1 indicating higher discriminatory ability.

An 80/20 training–testing data split was applied, with 80% of occurrence records used for model calibration and 20% for validation (Dyderski et al., 2025⁵²; Lu et al., 2025⁵³). 10,000 background points were used to characterise the available environmental space across the study area (Elith et al., 2010)⁵¹. Model uncertainty was assessed using the standard deviation across 10 bootstrap replicates, which quantifies variability in predictions across repeated model runs.

Percent contribution values provided by MaxEnt were used as the primary metric for comparing variable influence as they reflect the relative weight each predictor had in shaping model predictions (Lu et al., 2025)⁵³, with permutation importance and jackknife tests providing supplementary validation. Response curves were examined to assess the marginal effect of individual variables on predicted suitability, holding all other variables at their mean sample value (Thampan et al., 2025)⁵⁴.

Finally, binary habitat suitability maps were produced by applying the Maximum Training Sensitivity plus Specificity threshold (MTSS), which maximises the correct classification of presences and absences based on background points and has been identified as an effective threshold for presence-only data (Wang et al., 2024)⁵⁵.

2.5 Climatic Niche Overlap Analysis

Climatic niche overlap was quantified using the ‘PCA-env’ framework of Broennimann et al. (2012). The PCA was implemented using the *ade4* package in R (Dray and Dufour, 2007)⁵⁶. The environmental space was characterised by principal components derived from the five bioclimatic

variables used in the SDM (BIO2, BIO5, BIO11, BIO12, BIO15) and elevation derived from the DEM. Elevation was included due to its ecological relevance and because PCA accommodates for correlated predictors. The PCA was calibrated on 10,000 randomly sampled background pixels from the study area. The first two principal components, which captured the majority of environmental variation, were used to define a shared two-dimensional climatic space, onto which species occurrence records were projected. Following Broennimann et al. (2012)²⁸, a 100×100 cell lattice was used to bound the climate space, and kernel density smoothing was applied to estimate the relative density of species occurrences across climate space and reduce sampling bias, implemented using the *ecospat* package (Di Cola et al., 2017)⁵⁷.

Niche overlap between species was quantified using Schoener's D (0 = no overlap; 1 = complete overlap), and the statistical significance of these overlap values was evaluated using two randomisation tests with 100 permutations implemented in the *ecospat* package (Di Cola et al., 2017⁵⁷; Warren et al., 2008²⁵). The Niche Equivalency Test assesses the null hypothesis that the species' niches are identical; rejecting this ($p < 0.05$) indicates that differences between their climatic niches are statistically significant. The Niche Similarity Test assesses the null hypothesis that niches are no more similar than would be expected by chance given the environmental background available to each species. A significant result ($p < 0.05$) indicates that the niches are more similar than expected by chance (Xian et al., 2023)²⁹.

2.6 Future Climate Projections

Future climate projections were obtained from the CHELSA v2.1 dataset which provides bioclimatic projections for three CMIP6 Shared Socioeconomic Pathways: SSP1-2.6, SSP3-7.0

and SSP5-8.5 (Karger et al., 2017)⁴². SSP1-2.6 represents a low-emissions, sustainability-focused pathway with strong mitigation and relatively limited warming (~ 2.6 W/m²) by 2100. SSP3-7.0 reflects a medium-to-high emissions pathway characterized by weak international cooperation and continued reliance on fossil fuels (~ 7.0 W/m² by 2100). SSP5-8.5 represents a very high-emissions, worst-case scenario, fossil-fuel intensive pathway with strong radiative forcing (~ 8.5 W/m²) by the end of the century (O'Neill et al., 2017)⁵⁸.

All available CMIP6 future climate layers were downloaded for two time periods (2041-2070 and 2071-2100) in order to capture both mid-century and longer-term climate trajectories. Ensemble projections were calculated as the mean across all five CMIP6 GCMs available from CHELSA (GFDL-ESM4, IPSL-CM6A-LR, MPI-ESM1-2-HR, MRI-ESM2-0, UKESM1-0-LL), to reduce individual model bias and provide more robust estimates of future conditions (O'Neill et al., 2017⁵⁸; Dyderski et al., 2025⁵²).

2.7 Calibration Extent Sensitivity Analysis

To assess the influence of calibration extent on model predictions, two additional models were developed for *Acacia tortilis* using progressively broader domains. This enabled comparison across three extents (Figure 2):

1. Local extent: target range (original study area used for all species).
2. Intermediate extent: a regional domain approximating the Saharo-Arabian phytogeographic zone, including the Sinai Peninsula and adjacent parts of the Arabian Peninsula and North Africa

3. Wide extent: a broad African domain approximating the full observed climatic range of the species.

Figure 3. Calibration extents used for species distribution modelling of *Acacia tortilis*:
a) Local, b) Intermediate, c) Wide

This sensitivity analysis was conducted only for *A. tortilis* because this species has a wide geographic distribution and is the most thermophilic species, with the ability to thrive in much higher temperatures than those available within the local study area (Uni et al., 2023a)⁵⁹. Therefore, the wide extent aims to capture the full thermal range of the species to reduce the risk of niche truncation and extrapolation in future projections (Guisan et al., 2025)³².

However, given that *A. tortilis* peripheral populations of the Negev occur within a distinct phytogeographic and climatic context relative to their core African distribution (Shmida and Aronson, 1986)⁸, the intermediate extent was selected as a regional domain, informed by phytogeographical boundaries.

Occurrence data obtained from GBIF was thinned to one occurrence per grid cell. For the expanded extents, environmental variables were downloaded at five times coarser spatial resolution than the original 1km CHELSA data, while the local extent retained the original 1km data resampled to a 100m analysis grid. Only climatic predictors were included in the broader extent models as edaphic variables and distance-to-streams are not meaningful at coarser spatial resolutions. All models were subsequently projected onto the local study area to enable direct comparison of present-day suitability and future projections.

339

340 **3. Results**

341 **3.1 Final Model Results**

342 **3.1.1 Model Output**

343 The relative roles of environmental predictors varied largely among the three species (Table 2).

344 **Table 2.** Relative percent contribution of each environmental variable to the MaxEnt models and model
345 AUC values.

Variable	<i>A. tortilis</i>	<i>A. raddiana</i>	<i>A. pachyceras</i>
	Percent contribution in MaxEnt (%)		
BIO2	4.5	3.2	2.4
BIO5	73.3	41.3	10.1
BIO11	7.1	2.3	0
BIO12	3.5	35.3	22.4
BIO15	2.3	1.2	26.2
Sand Content	3.6	7.7	0.4
Bulk Density	5.3	2.5	10
Distance to Streams	0.4	6.6	28.5
	AUC		
	0.948	0.873	0.994

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Temperature emerged as the dominant driver of the distribution of *A. tortilis*. The distribution of *A. raddiana* was largely determined by both temperature and precipitation gradients, with a moderate role of distance to streams. In contrast, *A. pachyceras* was primarily influenced by distance to streams and precipitation-related variables.

3.1.2 Environmental Variables: Spatial Patterns and Responses

Environmental predictors display clear spatial gradients across the study area (Figure 4). Temperature variables (BIO5 and BIO11) are highest in the eastern Arava Valley and the south, and generally lower across the central Negev and Highlands. Annual precipitation (BIO12) shows a pronounced latitudinal gradient, decreasing from wetter conditions in the north to drier conditions in the south. Although elevation was not included as a predictor in the final models, it strongly influences climatic gradients and provides important spatial context for species distributions, especially the low-lying Arava Valley and elevated Negev Highlands, closely aligning with temperature patterns (Figure 4(i)).

CHELSA ensemble projections across all future scenarios indicate increasing temperatures across the study area and overall declines in annual precipitation. Future bioclimatic change is displayed in Figure 4(a-e), using one representative future scenario to demonstrate the prevailing projected trajectory of climate change across the region.

Figure 4. Spatial distribution of environmental variables across the study area. Panels a–h show predictor variables used in the model. Panel i (elevation) is included for context but not used as a model predictor. Inset maps show late-century (2071-2100) projections for bioclimatic variables under SSP3-7.0, as a representative example of future climatic change.

369

370 Response curves reveal differences in how each species responds to environmental gradients
 371 (Figure 5). Suitability for *A. tortilis* increases with higher maximum temperatures (BIO5), whereas
 372 *A. raddiana* maintains high suitability across a broader BIO5 range. *A. pachyceras* shows higher
 373 suitability at lower BIO5 values, although suitability remains high at warmer temperatures,
 374 showing that no upper thermal threshold is captured by the model.

375 Responses to BIO11 are similar for *A. tortilis* and *A. raddiana*, with suitability increasing at higher
 376 BIO11 values, although there is an unexpected sharp decline at the highest values, potentially
 377 resulting from a model artifact rather than a true ecological limit. For *A. pachyceras*, BIO11 shows
 378 a flat response curve, reflecting its 0% contribution to the model (Table 2).

379 Precipitation variables further differentiate species responses, with all species showing higher
 380 suitability under drier conditions but with varying degrees of sensitivity. *A. pachyceras* shows
 381 highest suitability restricted to low BIO12 values, while *A. tortilis* remains suitable across a wider
 382 precipitation range, and *A. raddiana* shows an intermediate response. Precipitation seasonality
 383 (BIO15) is the highest contributing variable for *A. pachyceras* and its response curve shows a clear
 384 peak in suitability at intermediate seasonality values. This pattern is reflected spatially, as its
 385 distribution closely aligns with areas of intermediate BIO15 values shown in Figure 4(e).

386 Species show higher suitability at moderately sandy soils and lower bulk density, with more
 387 extreme responses for *A. pachyceras*. However, variables with low contribution, such as sand
 388 content for *A. pachyceras*, are unlikely to represent strong ecological drivers and should not be
 389 over-interpreted. While edaphic variables provide useful context, the analysis is primarily focused

on climatic influences which represent the dynamic drivers of species' niche responses to climate change.

Figure 5. Comparative response curves of variables across species models

3.2 Suitability Predictions

3.2.1 Present-day suitability

Present-day suitability predictions reveal distinct spatial distributions across the three species, with *A. tortilis* concentrated along the eastern Arava Valley, *A. raddiana* showing a broader and more widespread distribution spanning both central and eastern areas, and *A. pachyceras* restricted to a smaller, more central area of the Negev Highlands (Figure 6). Model predictions showed low uncertainty across all three species, with standard deviation values generally below 0.15 in areas of predicted suitability and close to zero elsewhere, indicating strong agreement across model replicates.

Figure 6. Present-day binary suitability maps for a) *A. tortilis*, b) *A. raddiana*, and c) *A. pachyceras* using each model's unique Maximum Training Sensitivity plus Specificity (MTSS) threshold (0.166, 0.348, and 0.119, respectively).

3.2.2 Future Projections Across Scenarios

Across all species, projections for 2041–2070 show expansion of suitable habitat primarily in central and western areas as well as contraction in the east. By 2071–2100, gains are reduced and overall habitat loss increases, particularly under SSP5-8.5, leaving suitability restricted to smaller areas in the western Negev.

The magnitude of change varies among species. *A. raddiana* shows the largest mid-century expansion of suitable habitat across scenarios. *A. tortilis* exhibits more redistribution than net expansion, with gains in western areas offset by losses in eastern regions. *A. pachyceras* follows a similar trend, but with the least extensive overall changes.

Figure 7. Projected suitability changes for *A. tortilis*, *A. raddiana*, and *A. pachyceras* under SSP1–2.6 (best-case scenario) and SSP5–8.5 (worst-case scenario) for 2041–2070 and 2071–2100. The same species-specific MTSS thresholds used for the present-day binary maps were applied. Colours indicate loss (pink), gain (blue), and areas remaining suitable in both present and future (green).

The SSP3-7.0 projections (not shown) followed the same direction of change, representing an intermediate shift between SSP1-2.6 and SSP5-8.5, suggesting a progressive response to increasing emissions.

3.3 Niche Overlap Analysis

3.3.1 Climatic Niches in PCA Space

The PCA1-PCA2 axes and variable loadings show that PC1 is strongly weighted by precipitation variables (BIO12 and BIO15), while PC2 broadly reflects the temperature–elevation gradient. *A. raddiana* shows the widest spread across environmental gradients, representing a broader climatic niche. The niche of *A. tortilis* is largely nested within that of *A. raddiana*, concentrated at lower PC2 values consistent with hotter, low-elevation environments. *A. pachyceras* is more tightly clustered at low PC1 and low-to-mid PC2 values, occupying a small subset of the climate space used by the other species, representing a narrower niche breadth.

Figure 8. PCA of environmental space across the study area. **a)** Smoothed convex hulls around the main cluster of occurrence points representing the climatic niches of *A. tortilis* (red), *A. raddiana* (blue), and *A. pachyceras* (purple). **b)** Environmental variable loadings on PC1 and PC2; numerical variable loadings are provided in Appendix A.

PC1 and PC2 explained 82.6% of total environmental variation, indicating that most climatic structure was captured in two dimensions. Adding PC3 increased cumulative variance explained to 93.7%, but niche patterns in PC1–PC3 space were highly similar, confirming that PC1–PC2 adequately represents interspecific niche relationships.

3.3.2 Quantitative Niche Overlap Metrics

Table 3. Climatic niche overlap between species pairs quantified by Schoener’s D (0 = no overlap, 1 = complete overlap), and results of niche equivalency and similarity tests. Significant result (p<0.05) indicated in bold

Species Pair	Schoener’s D	Equivalency p-value	Similarity p-value
<i>A. tortilis</i> vs <i>A. raddiana</i>	0.172	0.406	0.307
<i>A. tortilis</i> vs <i>A. pachyceras</i>	0.177	0.455	0.010
<i>A. raddiana</i> vs <i>A. pachyceras</i>	0.016	0.554	0.099

All species pairs show relatively low overlap (Table 3), although notably *A. tortilis* and *A. pachyceras* show the highest overlap (D=0.177), and significant niche similarity. This is surprising since their geographic distributions do not overlap. The similarity between other species pairs was insignificant and equivalency tests were non-significant for all pairs, thereby failing to reject the null hypothesis of niche equivalency.

3.4 Calibration Extent for *A. tortilis*

3.4.1 Mitigating Niche Truncation at the Local Scale

Projected increases in maximum temperature (BIO5) exceed the current maximum observed within the local study area (39.25°C), particularly under high-emission scenarios. This indicates

that future projections involve novel climatic conditions not represented in the model training data, especially in the eastern Arava Valley where temperatures are already highest in the study area. To address this, the wide calibration extent was designed to capture the full range of thermal conditions under which *Acacia tortilis* is known to occur, incorporating occurrence records with BIO5 values up to 44.75°C. For the intermediate extent, the maximum BIO5 value at an occurrence record is 41.66°C. This extent acts as a middle ground, expanding the thermal range beyond the local study area while limiting excessive geographic expansion.

Figure 9. Model calibration extent for *A. tortilis*: a) local, b) intermediate and c) wide, overlaid on BIO5 maps. Occurrence points in red show locations where BIO5 exceeds the local maximum; black points fall within the local BIO5 range.

3.4.2 Model Performance and Suitability Across Extents

Table 4. Model AUC across calibration extents

Extent	AUC of model
Local	0.948
Intermediate	0.909
Wide	0.837

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480 Expanding the calibration extent reduced present-day model performance, with AUC decreasing
 481 as extent increased (Table 4). Furthermore, present-day suitability predictions differed
 482 substantially across extents (Figure 10). The model based on the local extent closely aligned with
 483 known occurrence records, while the intermediate-extent and wide-extent models suggested
 484 progressively broader suitability, including areas in the north and west where the species is absent.

485

486 **Figure 10.** Predicted present-day suitability for *Acacia tortilis* from models calibrated with different
 487 extents: a) local, b) intermediate and c) wide; all projected onto the local study area.

488

489

490 **3.4.3 Future Suitability Projections**

491 All models predict suitability to shift further westward with more extreme climatic scenarios,
 492 however the magnitude of these changes varied among calibration extents (Figure 11). The local
 493 model projects the most drastic changes, whereas the wide-extent model shows the least change
 494 across scenarios, with contraction of suitability in the east occurring only in the worst-case scenario
 495 for the wide-extent.

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Figure 11. Binary maps of predicted suitable habitat for *Acacia tortilis* under present climate conditions and late-century projections (2071–2100) for two emission scenarios: SSP1-2.6 (best-case) and SSP5-8.5 (worst-case) across model calibration extents. Binary suitability used extent-specific MTSS thresholds.

4. Discussion

4.1 RQ1 – Present-day Species Distributions and Climatic Niches

4.1.1 Interpreting SDMs: Environmental drivers of species distributions

The SDMs for all three species showed high predictive performance, indicating that their distributions are strongly structured by environmental conditions. However, the dominant predictors differed among species, suggesting distinct ecological constraints and climatic niches.

For *A. tortilis*, the model was strongly dominated by BIO5 (maximum temperature of the warmest month), indicating that temperature conditions are the primary constraint on its distribution. Suitability declined sharply at cooler temperatures, reflecting their known thermophilic nature and restriction to hot desert environments (Uni et al., 2021)²¹. This explains the species' absence from the central Arava, (fig) where altitude is raised and temperatures are slightly warmer, and from the whole Negev, for the same reason. The minimal contribution of distance to streams is consistent with evidence that *A. tortilis* has high water-use efficiency and is well adapted to environments with more infrequent water pulses and low soil moisture (Uni et al., 2023b)²². Suitability remained high across a broad precipitation gradient, reflecting its distribution into northern wetter areas as long as temperature is high, the conditions of the Arava in the east (Figure 4(d, b)).

The model for *A. raddiana* reflects its widespread distribution and broader ecological niche (Ward et al., 2011)⁶⁰, with strong contributions from both temperature (BIO5) and precipitation (BIO12) suggesting its distribution is influenced by a balance of climatic factors rather than a single dominant constraint. The importance of precipitation likely reflects the strong north–south precipitation gradient across the study area, as *A. raddiana* occurs widely across the south but is absent from wetter northern areas. Response curves show that *A. raddiana* maintains high suitability across a broader range of temperatures than *A. tortilis*, reinforcing its wider climatic tolerance. Distance to streams shows a higher contribution than *A. tortilis*, consistent with evidence that *A. raddiana* is less drought tolerant and more associated with main channel environments where water availability is higher (Uni et al., 2023b)²².

For *A. pachyceras*, precipitation variables and distance to streams were the strongest predictors, while temperature variables provided limited contributions. Although the species is associated with higher elevations and cooler environments, weak contributions for temperature in the model suggest that it may not be directly constrained by thermal limits to the same degree as *A. tortilis*. Instead, its strong association with proximity to streams indicates greater dependence on local water availability. Experimental evidence supports this interpretation. When Uni et al. (2021)²¹ grew all three species under uniform, hot desert conditions in a controlled irrigation experiment, *A. pachyceras* showed the strongest growth and greener canopies when provided with high irrigation. The species' success in a hot environment when provided with sufficient water suggests that temperature alone is not a strict physiological constraint, but water availability may be the key ecological constraint for this species.

However, the interpretation of SDMs must account for the statistical properties of the modelling framework, particularly for the *A. pachyceras* model. Relative Occurrence Area, defined as the

proportion of the study region occupied by a species, affects model performance (Tessarolo et al., 2021)⁶¹. Species with smaller Relative Occurrence Area often yield inflated performance metrics (AUC) because presence points occupy a narrow portion of environmental space, resulting in an increased proportion of correctly predicted background absences across the wider background. Therefore, the high AUC value for *A. pachyceras* model (0.994) likely reflects its small geographic range within the study area, rather than showing strong ecological representation. Its restricted range may also explain why some predictors became especially prominent. When the background extent in an SDM is large relative to the species' range, models tend to simplify and become dominated by a small number of variables that provide the strongest regional discrimination (VanDerWal et al., 2009)⁶². In the study area, BIO12 follows a clear north-south precipitation gradient, creating strong contrast between the dry southern habitat of *A. pachyceras* and the wetter northern background (Figure 4(d)). Similarly, BIO15 (Precipitation Seasonality) provides strong contrast because the species occupy a narrow band of intermediate BIO15 values relative to the broader variation across the study area. Furthermore, because climatic conditions are relatively uniform at small spatial scales, localised environmental variables may become relatively more important for distinguishing presences from background (Pearson and Dawson, 2003)⁶³. Thus, the prominence of distance to streams for *A. pachyceras* may reflect its genuine dependence on water proximity, but it may also be amplified by the statistical artifact caused by its restricted range.

Some response-curve features may also reflect SDM mechanisms rather than true ecological thresholds. MaxEnt applies regularisation to limit model complexity and reduce overfitting (Elith et al., 2010)⁵¹. As a result, response curves may show sharp declines in suitability at environmental extremes where data are scarcely represented, or flat responses for variables that contribute little to the model, which likely explains the response curves observed for BIO11.

4.1.2 Climatic niche relationships among species

SDM results offer some insight into ecological niche differentiation among species; *A. tortilis* appears primarily constrained by temperature, *A. pachyceras* shows stronger dependence on local water availability, and *A. raddiana* shows a broader climatic tolerance. However, given the modelling limitations mentioned, ecological interpretation should not rely solely on SDM variable importance. PCA provides an alternative framework for comparing species' niches while avoiding potential biases associated with SDM predictor contributions (Warren et al., 2008)²⁵. By reducing variables into major climatic gradients, it creates a shared environmental space in which climatic niche overlap can be quantified.

A. raddiana overlaps geographically with both other species, yet low Schoener's D values indicate low climatic niche overlap. This likely reflects differences in niche breadth, which describes the range of environmental conditions a species can tolerate or utilise (Slatyer et al., 2013)⁶⁴. *A. raddiana* is the most widespread species and occupies a broad range of environmental conditions, whereas *A. tortilis* and *A. pachyceras* are more climatically restricted with narrower, more specialised niches. This is evident in the PCA, where the niches of *A. tortilis* and *A. pachyceras* appear as subsets nested within that of *A. raddiana*. The particularly low Schoener's D (showing niche overlap) between *A. raddiana* and *A. pachyceras* (D=0.016) likely reflects the contrast in niche breadth between these species, resulting in low climatic niche overlap despite geographic sympatry.

Although overlap values were low, equivalency tests failed to reject the null hypothesis for all species pairs, meaning there is insufficient evidence to conclude that their climatic niches are

significantly distinct. Notably, the only statistically significant result was the niche similarity test between *A. tortilis* and *A. pachyceras*, which also showed the highest overlap (Schoener's D) value. This is surprising as they do not overlap geographically and suggests that these two species may share more similar fundamental climatic requirements than their current distributions imply. Their geographical separation has generally been attributed to the elevation–temperature gradient, with *A. tortilis* confined to hotter lowlands and *A. pachyceras* to cooler high-elevation areas (Uni et al., 2021)²¹. The PCA does capture this pattern, with *A. pachyceras* concentrated at a slightly higher PC2 range (lower temperature, higher elevation), however its niche is still nested within that of *A. tortilis*, signifying climatic niche overlap.

Combining the SDM and climatic niche results provides insight into the relationship between the two species. The SDM response curves indicate that *A. tortilis* distribution is strongly temperature-limited (BIO5). However, *A. pachyceras* retains high predicted suitability at higher BIO5 despite being largely absent from these warmer environments (Figure 5(b)). In other words, the model does not indicate that *A. pachyceras* is incapable of occupying warmer environments to the same extent that *A. tortilis* appears incapable of occupying cooler areas. This reinforces the view that temperature is not the primary limitation for *A. pachyceras*.

Their significant climatic niche overlap and these SDM results raise the possibility that their geographic separation may be driven by factors other than climatic constraints. One possible hypothesis is competitive exclusion, whereby one species restricts the realised distribution of another with similar ecological requirements (Connell, 1961)⁶⁵. *A. pachyceras* may be physiologically capable of persisting in hotter lowland environments but excluded by *A. tortilis* under these conditions. Conversely, at higher elevations where temperature limits *A. tortilis*, reduced competitive pressure may allow *A. pachyceras* to persist. This would help explain why

the two species show climatic similarity without geographic co-occurrence. Because correlative SDMs do not explicitly incorporate interspecific competition, they may overestimate species' distributions where their realised ranges are constrained by biotic interactions (McPherson and Jetz, 2007)³³. The projected suitable areas for *A. pachyceras* in this study may reflect its fundamental niche, defined as the range of conditions it could occupy in the absence of biotic constraints, rather than its realised distribution shaped by competition and other biotic factors (Wiens et al., 2009)⁶⁶.

4.2 RQ2 – Future Distribution Projections

Future projections indicate a redistribution of suitable habitat toward central and western parts of the Negev during the 21st century, with moderate mid-century expansion followed by increasing contraction and fragmentation under late-century high-emission scenarios. This shift suggests that moderate warming may initially create more climatically suitable areas, but as climatic stress intensifies, environmental conditions may exceed physiological tolerance thresholds and ultimately result in range contraction.

Differences across scenarios highlight the importance of climate trajectory. The Negev is projected to become warmer and drier, reflected in the CHELSA projections used in this study which show declining precipitation and rising temperatures (Figure 4), trends that intensify under higher-emission scenarios. In the models, low-emission scenarios (SSP1-2.6) predict modest shifts and westward expansion, whereas high-emission pathways (SSP3-7.0 and SSP5-8.5) produce greater habitat loss and fragmentation. This is likely driven by the crossing of ecological aridity thresholds,

beyond which species persistence becomes unstable and habitat loss accelerates (Berdugo et al., 2021)¹³. Given that *Acacia* survival depends on episodic flood-driven recharge and rainfall events for seedling recruitment (Wiegand et al., 2003⁶⁷; Shrestha et al., 2003¹⁹), a continued reduction in runoff-generating events would reduce recharge opportunities and limit recruitment success. *Acacia* declines in the southern Negev have been attributed to warming and drying (Stavi et al., 2014)³, suggesting these survival thresholds may have already been breached there. The shift from overall expansion under low-emission scenarios to contraction under high-emission scenarios suggests the presence of critical climatic thresholds between emission pathways. This highlights the importance of emissions trajectories in determining future outcomes, with habitat viability being contingent on staying below high-emission limits.

Late-century predictions show increasing habitat loss with retreat from eastern and southern regions, particularly for *A. tortilis* and *A. raddiana*. However, the extremity of these changes in local-scale models may be influenced by niche truncation resulting from the restricted climate range of the study area (Thuiller et al., 2005)⁶⁸. As both species occur across a broader range in Africa (Ba et al., 2002)⁶⁹, their full climatic niche is not captured within the local study area. Thuiller et al., (2005)⁶⁸ note that models calibrated on truncated extents may overestimate future range expansion as they have to extrapolate into non-analogue climates. Therefore, the westward redistribution, especially the most pronounced predictions for *A. tortilis*, should be interpreted cautiously as it is likely exaggerated.

A. pachyceras retains the smallest area of suitable habitat under future projections. This reinforces the view that range-restricted species are particularly vulnerable to habitat loss under climate change (Thuiller et al., 2005)⁶⁸. Furthermore, the smaller distance in its overall shifts may mean

that *A. pachyceras* is already confined to a narrow geographic range in which it can persist, whether constrained by climatic or biotic factors, with limited ability to expand elsewhere.

Even with overall increasing regional aridity, future projections show that the Highlands remain relatively cooler and wetter than surrounding lowlands (Figure 4). Consequently, projected climatic changes in this area are less likely to exceed ecological thresholds for persistence, explaining why future suitable habitat for all three species is consistently concentrated in this region. However, if the previously discussed competitive exclusion hypothesis applies, the overlapping suitability predicted in the Highlands may not be fully realised. Following the hypothesis, if *A. tortilis* shifts its distribution to the Negev Highlands, *A. pachyceras* could be competitively excluded, meaning its modelled future distribution may be overestimated. In fact, this species may even become extinct within the studied area.

4.3 RQ3 – Model Calibration Extent Sensitivity

Considering that the local-scale model is potentially constrained by niche truncation, *A. tortilis* was modelled across broader spatial extents to assess how the study area domain influences predictions. As extent increased, model performance (AUC) declined and the model predicted larger areas of suitable habitat in the target range, exceeding the species' current observed distribution. This aligns with findings that continental models tend to overestimate suitability when projected to regional margins, whereas regionally calibrated models better capture local ecological limits (Vale et al., 2013)³⁰. This happens because large extents incorporate diverse vegetation zones and a wide range of ecosystem processes which may not reflect the ecological conditions affecting a focal population (Anderson and Raza, 2010)⁷⁰. Species–environment relationships

have been found to vary geographically due to local adaptation, habitat shifts and differences in limiting factors across regions (McPherson & Jetz, 2007)³³. In this study, *A. tortilis* in the local target range represent peripheral populations occurring in a climatic regime that differs substantially from their African core (Ba et al., 2002)⁶⁹. Consequently, calibration across the wide extent integrates environmental relationships across multiple biogeographic contexts, likely producing overestimated suitability within the target range. The intermediate extent shows a closer alignment with the actual present-day distribution, likely because the calibration is restricted to a more coherent phytogeographic and environmental context.

However, both intermediate and wide models predicted suitability north of 32°N where *A. tortilis* does not occur. This is likely because expanded extents include occurrences under a broader range of climatic conditions, producing response curves with high suitability across a wider temperature range (BIO5 and BIO11). As a result, the model becomes more permissive, predicting suitability in areas beyond the species' observed northern limit, where climates may resemble conditions occupied by the species elsewhere in the wider range. This highlights how expanding the calibration extent alters the background environmental contrasts used by the model, leading to more generalised estimates of climatic suitability rather than capturing the specific local realised niche.

Results for future projections align with evidence from Anselmetto et al. (2024)³¹ that locally calibrated models predict greater magnitudes of future change. The authors highlight the key trade-off that while local models better reflect present-day realised distributions, they suffer from niche truncation when extrapolated to the future. This creates uncertainty in the accuracy of future predictions from the local model. Nevertheless, all models converge on a pattern of reduced suitability in eastern parts of the study area under severe warming scenarios. This suggests that

although *A. tortilis* is highly adapted to heat, extreme future temperatures will likely exceed its tolerance limits in the east. The fact that this climatic threshold is eventually revealed by all model calibrations shows that it is not just an artifact of niche truncation from the local model.

Finally, expanding calibration extent introduces additional uncertainty associated with global occurrence datasets. GBIF records are subject to spatial sampling bias, misidentification, and uneven survey effort (Beck et al., 2014)⁷¹. Taxonomic complexity within *Acacia*, particularly following its reclassification into *Vachellia* and *Senegalia*, further complicates accurate species identification in broad-scale datasets (Suleiman et al., 2017)⁹. Specifically, the classification of *A. pachyceras* remains taxonomically unresolved, with some authorities synonymizing it under *Vachellia gerrardii* subsp. *Negevensis* (Ragupathy et al., 2014⁷²; POWO, 2026⁷³). Here, *Acacia raddiana* is treated as a species distinct from *A. tortilis*, following its recognition in studies of the Middle East (Danin, 1992)⁷, although it has been previously classified as *A. tortilis* subsp. *raddiana* (Brenan, 1957)⁷⁴. This leads to records being stored under inconsistent names across different regions and time periods. Furthermore, limited monitoring and under-sampling in arid regions results in incomplete records (Chanachai et al., 2024)³⁷. These limitations create bias and inconsistency in occurrence data, reducing the reliability of broad-scale models.

Ultimately, restricting calibration extent to the local study area provides more realistic predictions and enables more reliable data across the three species, making it the most appropriate choice for examining Negev *Acacia* distributions. Importantly, the fact that all calibration extents show declining suitability under severe warming scenarios strengthens confidence that the projected eastern habitat loss represents a real climatic threshold rather than an artefact of local niche truncation.

4.4 Limitations and Future work

A key limitation of correlative SDMs is that they rely solely on statistical associations between occurrence data and environmental variables to infer species–environment relationships, without accounting for the underlying physiological and biological mechanisms that drive these relationships (Wilkinson et al., 2019)⁷⁵. For instance, the three *Acacia* species exhibit different water-use strategies and stomatal responses to drought which influence their tolerance to water stress (Uni et al., 2023b)²². By failing to represent these physiological traits, correlative SDMs may not accurately capture species’ true responses to environmental change. Mechanistic (process-based) or hybrid models, which explicitly incorporate physiological constraints and responses, could be used for future work to improve these predictions (Kearney and Porter, 2009)⁷⁶.

Correlative SDMs are also unable to incorporate biotic interactions that may strongly influence species distributions (Dolos et al., 2015)⁷⁷. Mistletoe infestation, seed predation by bruchid beetles and reductions in herbivore-mediated seed dispersal have all been linked to *Acacia* population decline as they affect mortality and recruitment (Wiegand et al., 1997)⁷⁸. In addition, interspecific interactions may shape species’ realised distributions, as hypothesised in this study for *A. tortilis* and *A. pachyceras*. Further investigation into their interaction could help clarify whether this contributes to their geographic separation. Joint Species Distribution Models offer a way to incorporate species co-occurrence interactions, but they typically require presence-absence or abundance data, rather than the presence-only records used in this study (Wilkinson et al., 2019)⁷⁵. Therefore, future research could improve predictive accuracy by integrating alternative modelling approaches and collecting more comprehensive occurrence data from surveyed sites.

A further limitation relates to the quality and consistency of occurrence data, as discussed, which introduces uncertainty into model predictions especially at broader extents, highlighting the importance of adopting local-scale approaches in future modelling efforts.

Finally, this study estimates potential climatic habitat suitability, however realised distributions may be constrained by dispersal limitation, land-use change, or anthropogenic barriers. Although acacia trees are legally protected in Israel (Armoza-Zvuloni et al., 2021)¹⁵, infrastructure development can inadvertently disrupt natural flood regimes and reduce water availability (Ward and Rohner, 1997)¹⁷. Future work could create more realistic projections by intersecting predicted suitable habitat with land-use and urban extent data to identify where redistribution is both climatically suitable and physically plausible.

5. Conclusions

This study investigated the environmental drivers shaping the present and future distributions of three *Acacia* species in the Negev using SDMs and climatic niche analysis. Results reveal that *A. tortilis* is primarily temperature-limited, *A. raddiana* exhibits a broader climatic niche, spanning a wide range of temperature and precipitation gradients, while *A. pachyceras* occupies the narrowest climatic niche and appears to be primarily influenced by water availability.

Despite their distinct geographic separation, *A. tortilis* and *A. pachyceras* showed significant niche similarity and overlap in PCA space, suggesting that climatic conditions alone may not fully explain their realised distributions. While model outputs indicate that *A. tortilis* is strictly bound to high temperatures, *A. pachyceras* shows no clear restriction to cooler conditions and temperature does not appear to be a primary limiting factor. Consequently, this study proposes that the absence

of *A. pachyceras* from warmer regions may be driven by competitive exclusion by *A. tortilis* in areas where their niches overlap. This warrants further investigation and underscores the need for using modelling frameworks that incorporate biotic interactions in future research.

Future projections indicate that suitable habitat may initially expand westwards under moderate mid-century warming, but contract substantially under higher-emission late-century scenarios as climatic conditions increasingly exceed species tolerance thresholds. The convergence of all model calibrations on eastern habitat contraction under severe warming confirms this as a robust ecological signal. The magnitude and timing of projected shifts remain uncertain, but the direction of change is consistent across model configurations.

This study also demonstrates that model predictions are highly sensitive to calibration extent. Broader extents produced more generalised climatic relationships and overestimated present-day suitability within the target range, a consequence of integrating environmental relationships across biogeographic contexts that do not reflect the distinct climatic and hydrological regime of these peripheral Negev populations. Local-scale calibration is therefore the most appropriate approach for modelling *Acacia* in the Negev, and necessary given the inconsistencies and limitations in global occurrence datasets.

Ultimately, by characterising species-specific climatic constraints and informing the selection of appropriate modelling frameworks, this study advances understanding of *Acacia* niche dynamics in the Negev and provides a basis for refining future projections. Given their role as keystone species in Negev desert ecosystems, accurate predictions of *Acacia* dynamics are essential for anticipating broader ecological change across this landscape and guiding future conservation priorities.

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Figures

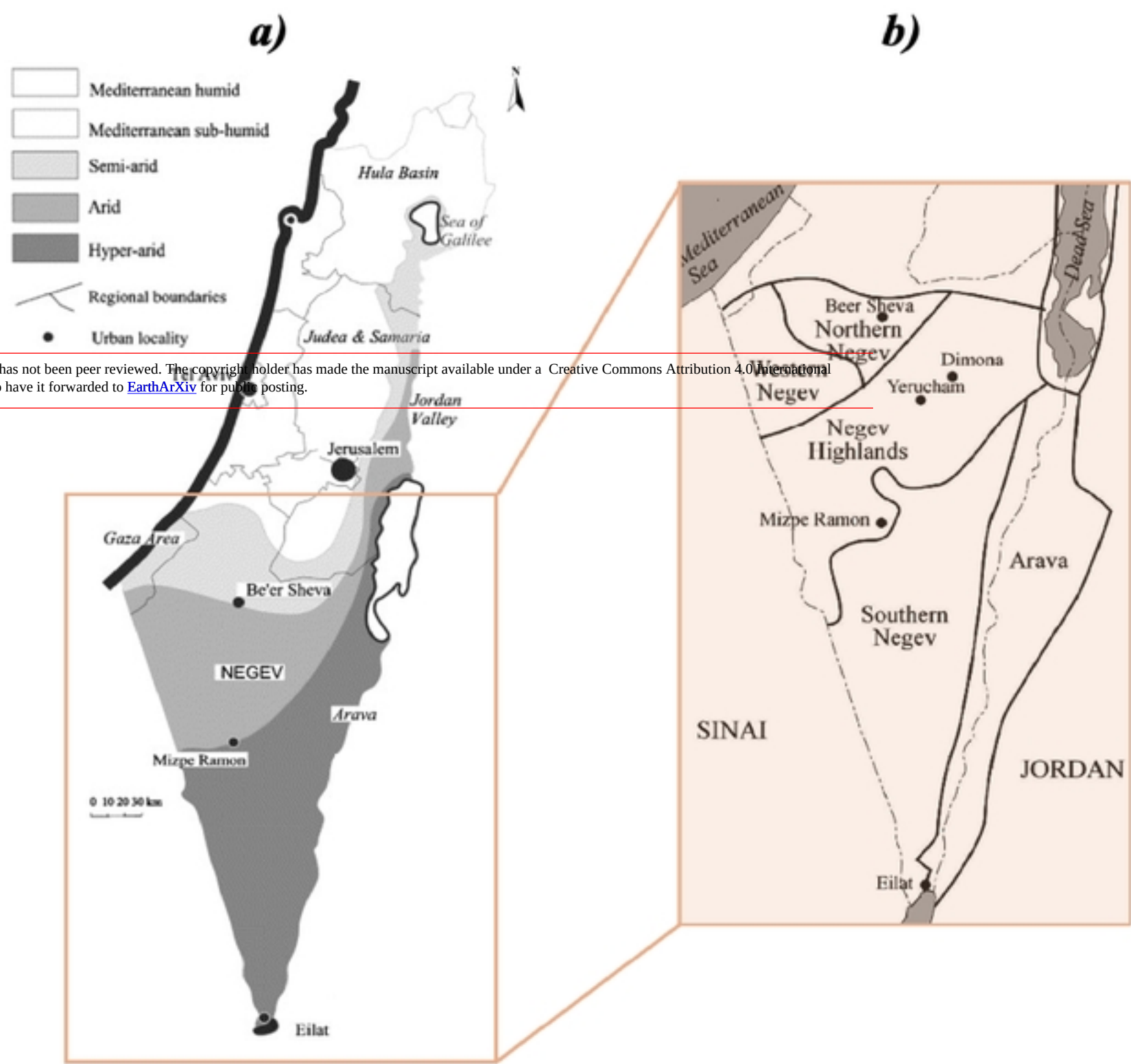


Figure 1. a) Climatic zones across Israel-Palestine demonstrating the north-south aridity gradient (modified from Portnov and Safriel, 2004)⁴. **b)** Map of the Negev desert and its subregions, featuring the Negev Highlands and the Arava Valley (modified from Collins-Kreiner and Wall., 2007)⁵

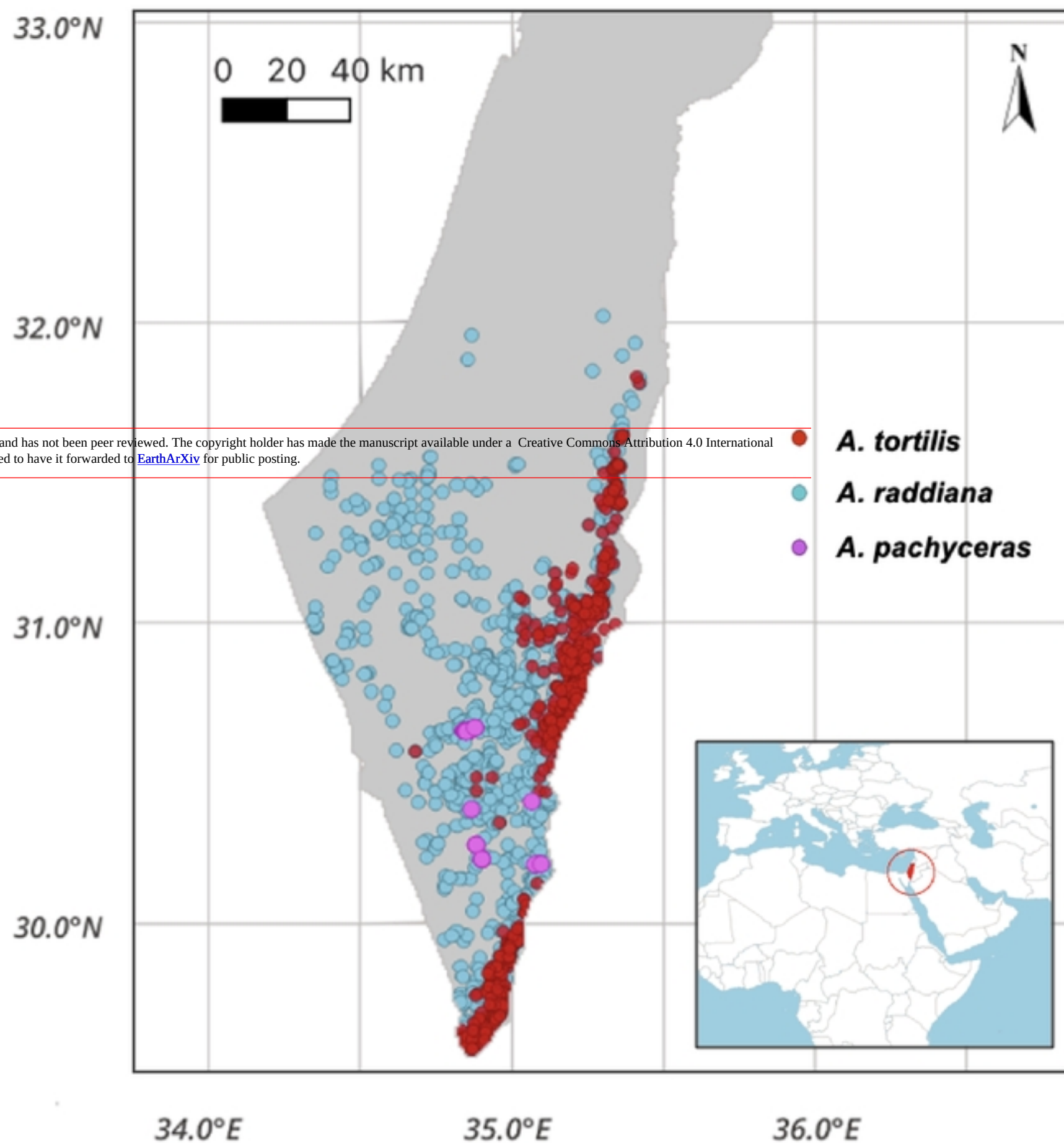


Figure 2. Study area with occurrence points of *Acacia tortilis*, *A. raddiana*, and *A. pachyceras*. Inset map shows position within the Middle East.

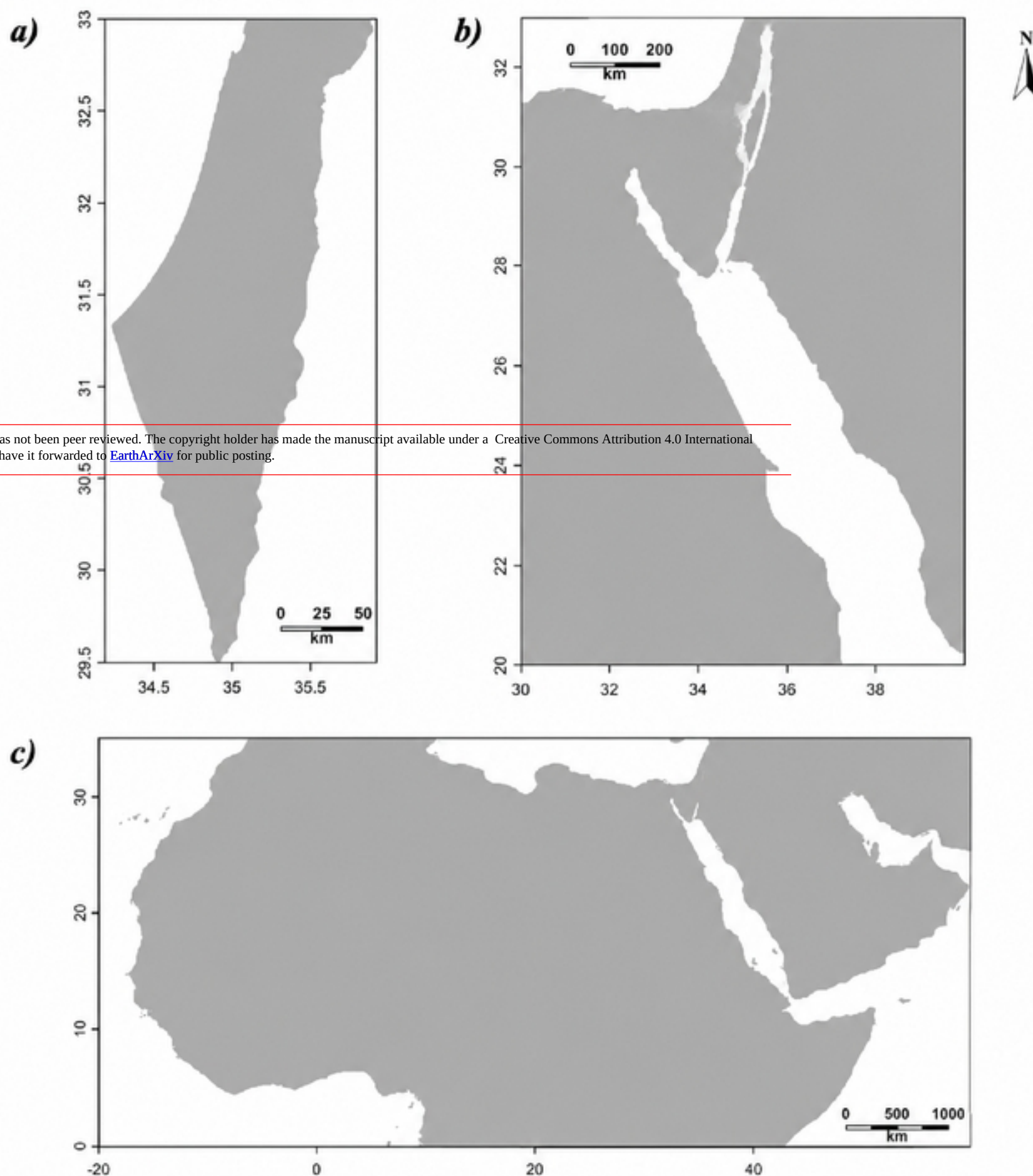


Figure 3. Calibration extents used for species distribution modelling of *Acacia tortilis*:

a) Local, b) Intermediate, c) Wide

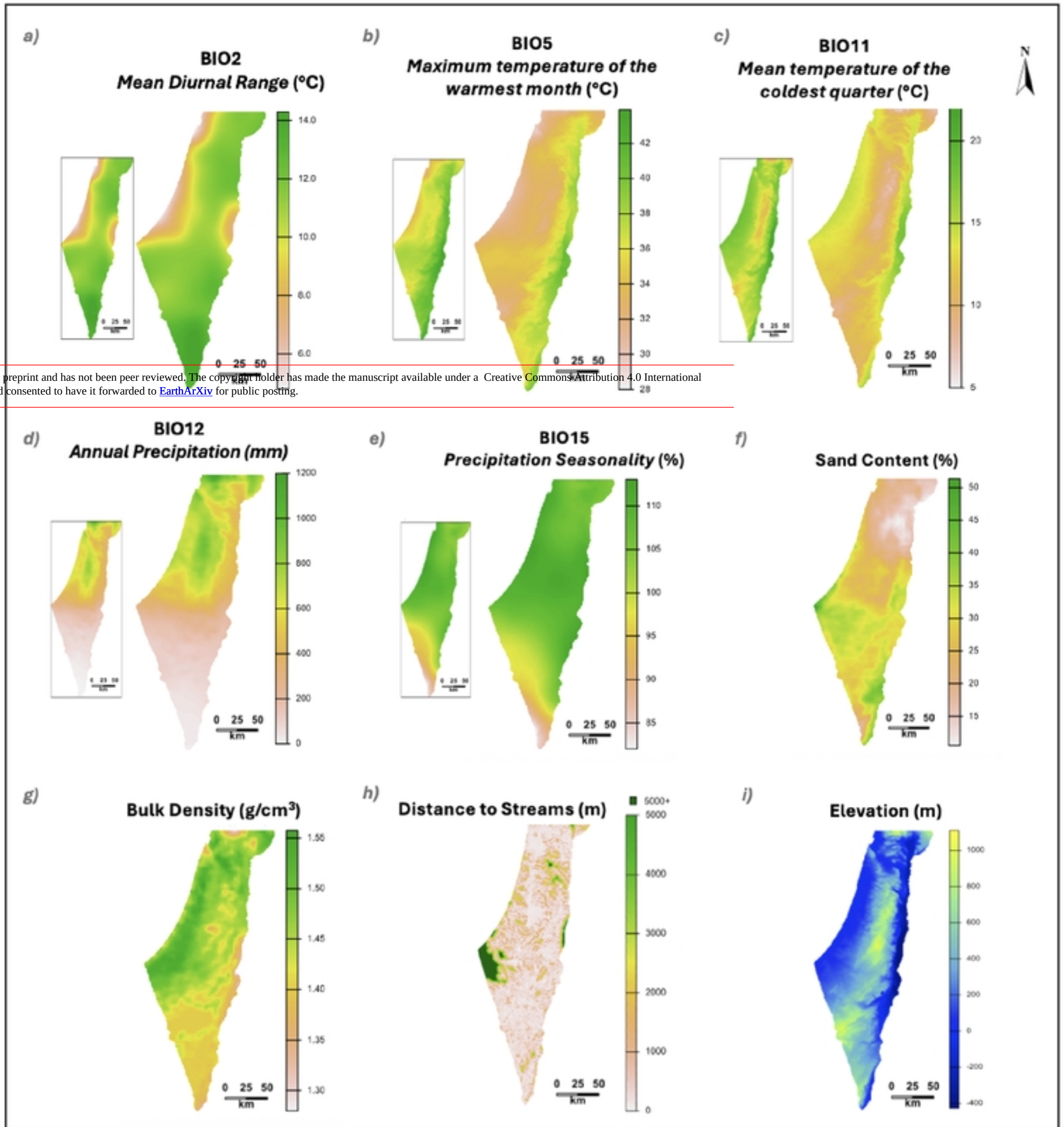


Figure 4. Spatial distribution of environmental variables across the study area. Panels a–h show predictor variables used in the model. Panel i (elevation) is included for context but not used as a model predictor.

Inset maps show late-century (2071-2100) projections for bioclimatic variables under SSP3-7.0, as a representative example of future climatic change.

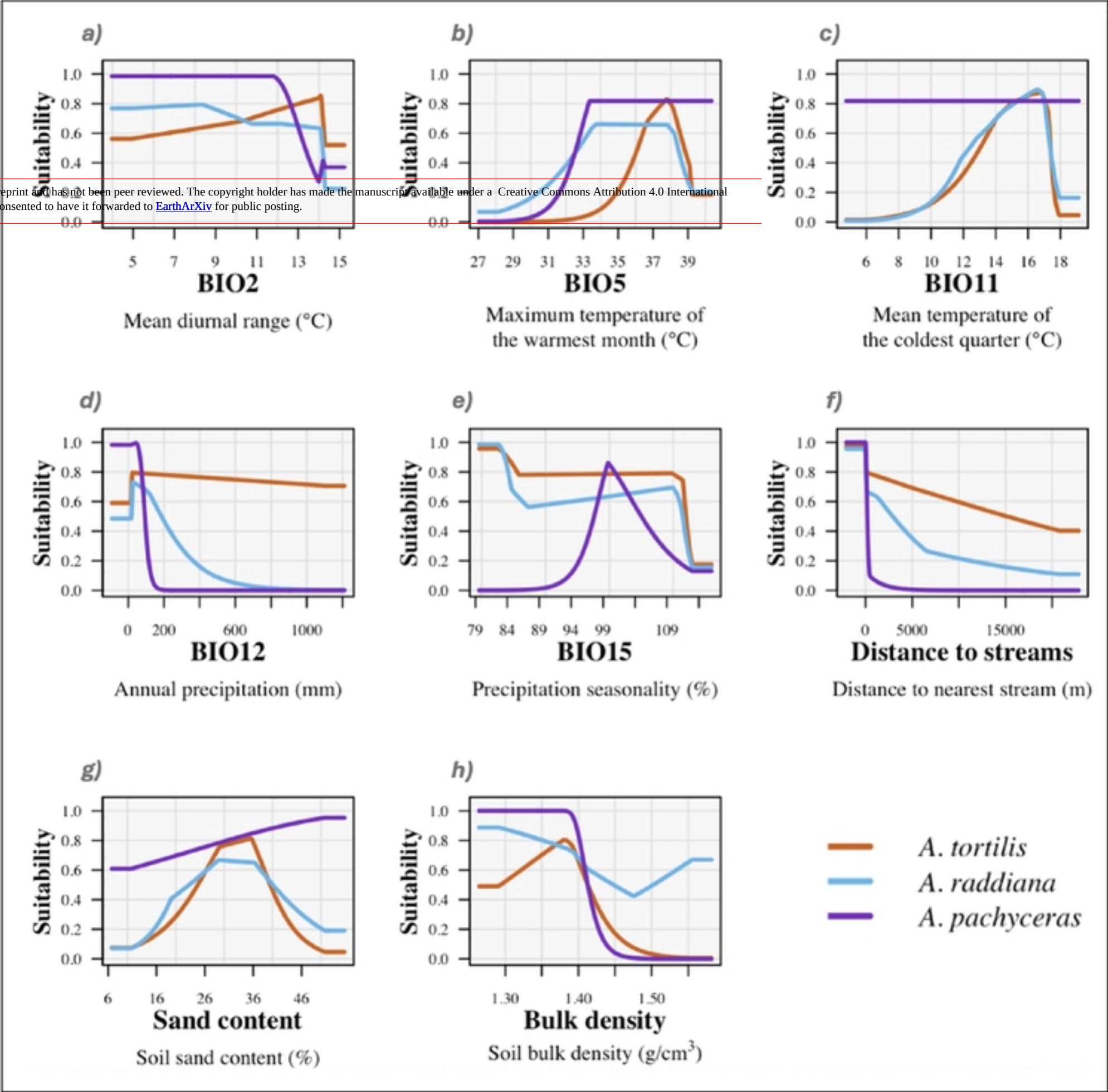


Figure 5. Comparative response curves of variables across species models

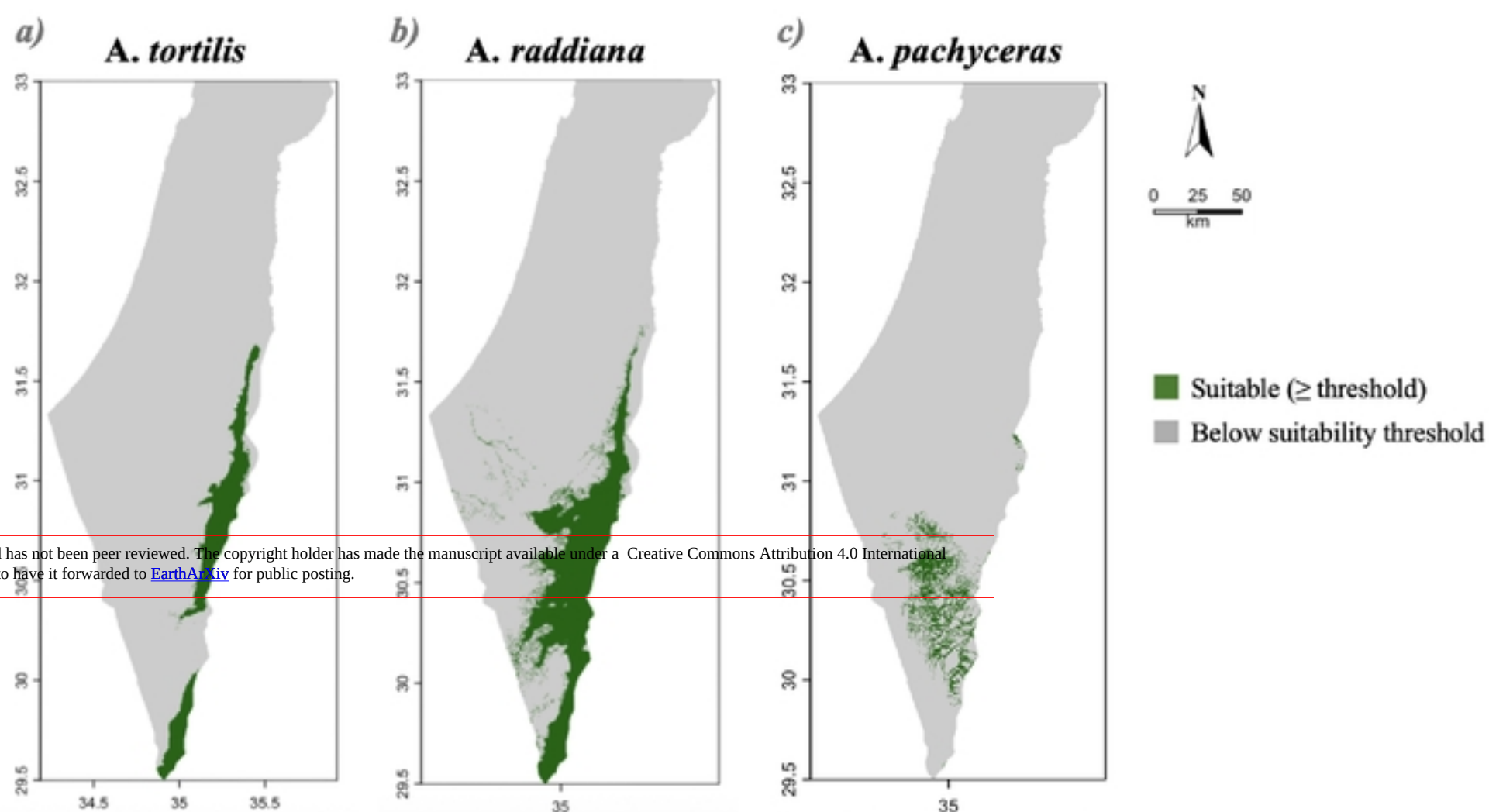


Figure 6. Present-day binary suitability maps for a) *A. tortilis*, b) *A. raddiana*, and c) *A. pachyceras* using each model's unique Maximum Training Sensitivity plus Specificity (MTSS) threshold (0.166, 0.348, and 0.119, respectively).

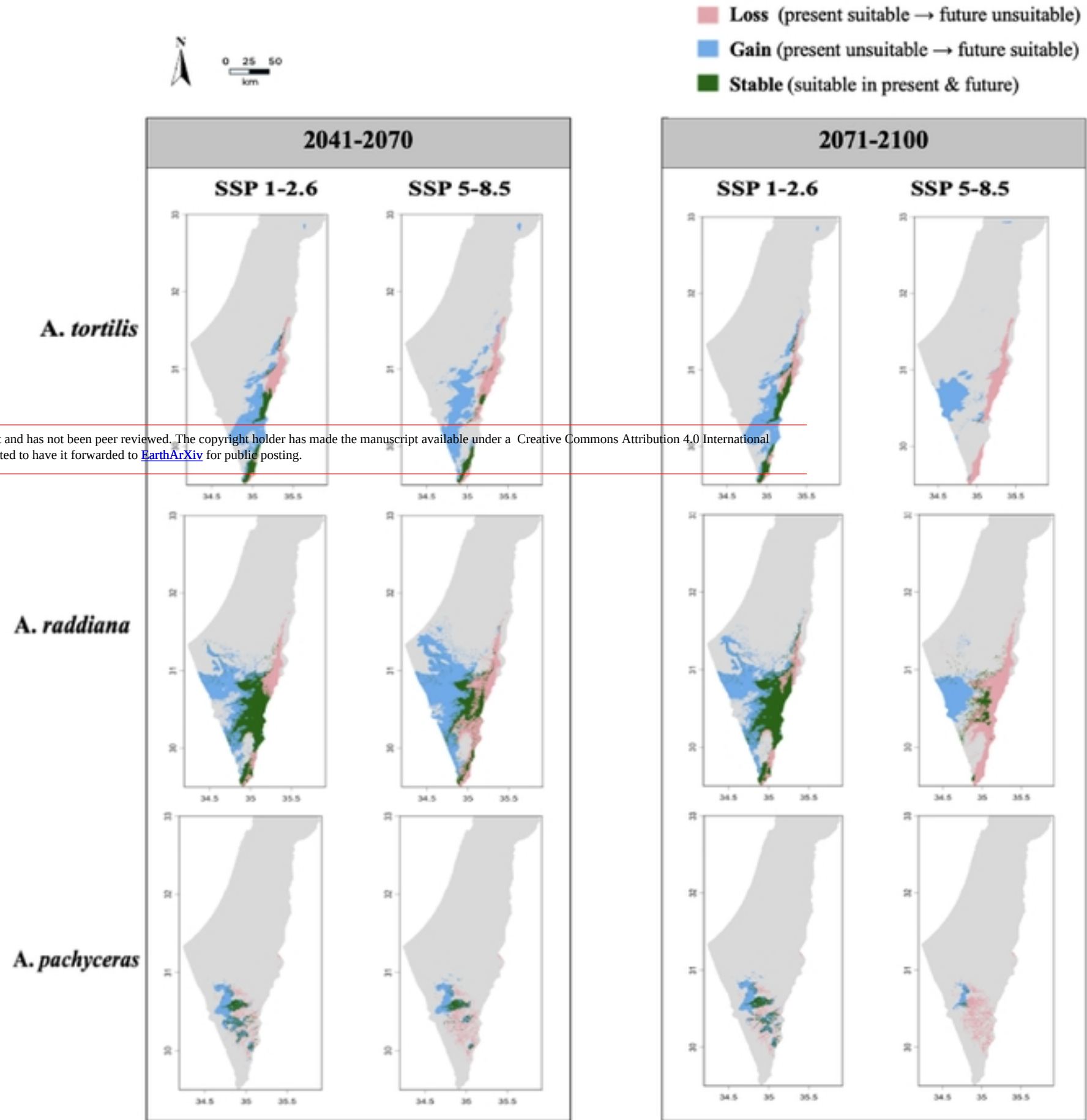


Figure 7. Projected suitability changes for *A. tortilis*, *A. raddiana*, and *A. pachyceras* under SSP1–2.6 (best-case scenario) and SSP5–8.5 (worst-case scenario) for 2041–2070 and 2071–2100. The same species-specific MTSS thresholds used for the present-day binary maps were applied. Colours indicate loss (pink), gain (blue), and areas remaining suitable in both present and future (green).

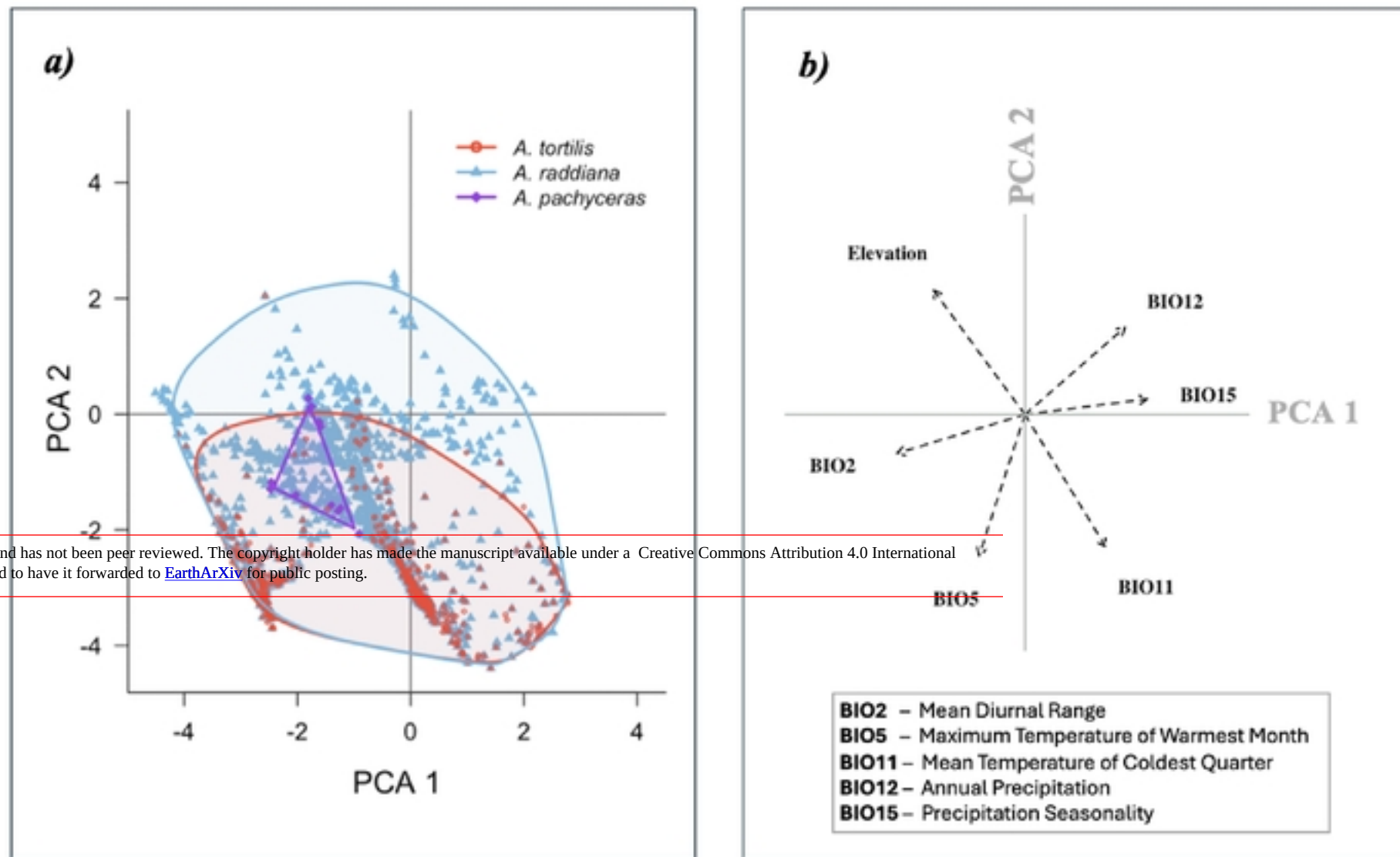


Figure 8. PCA of environmental space across the study area. **a)** Smoothed convex hulls around the main cluster of occurrence points representing the climatic niches of *A. tortilis* (red), *A. raddiana* (blue), and *A. pachyceras* (purple). **b)** Environmental variable loadings on PC1 and PC2; numerical variable loadings are provided in Appendix A.

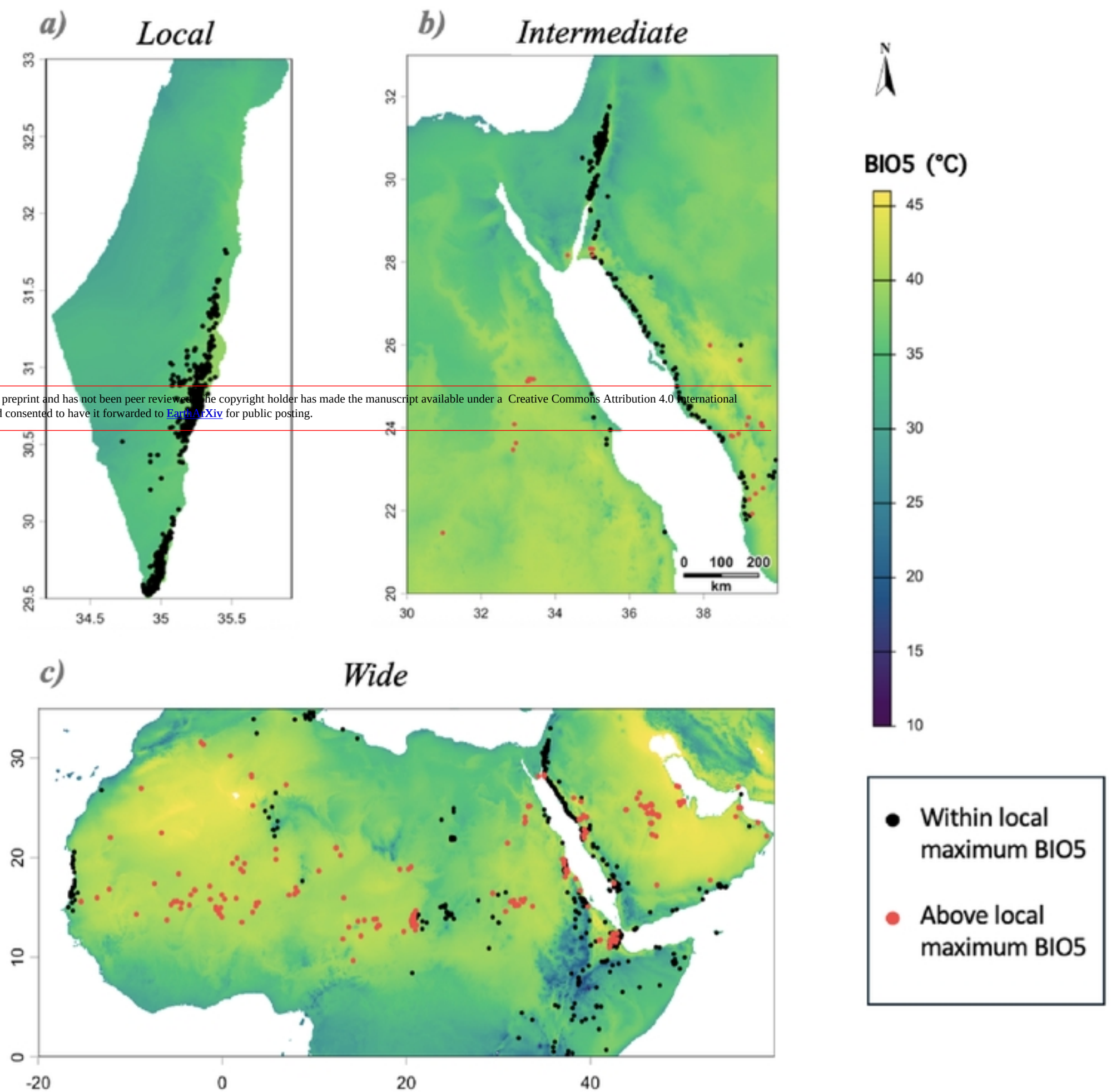


Figure 9. Model calibration extent for *A. tortilis*: a) local, b) intermediate and c) wide, overlaid on BIO5 maps. Occurrence points in red show locations where BIO5 exceeds the local maximum; black points fall within the local BIO5 range.

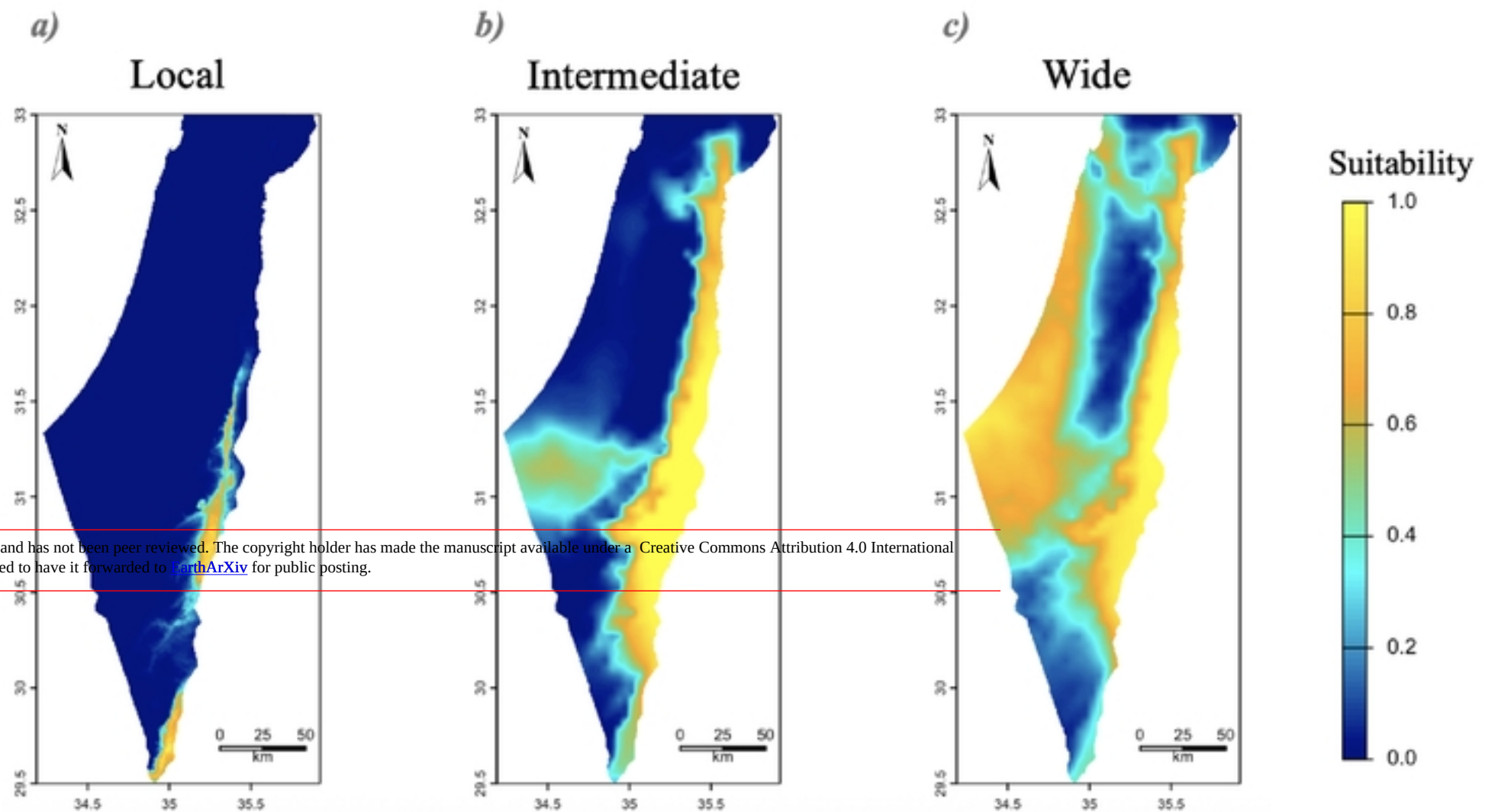


Figure 10. Predicted present-day suitability for *Acacia tortilis* from models calibrated with different extents: a) local, b) intermediate and c) wide; all projected onto the local study area.

Local

Intermediate

Wide

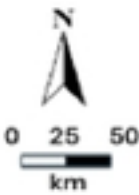


Figure 11. Binary maps of predicted suitable habitat for *Acacia tortilis* under present climate conditions and late-century projections (2071–2100) for two emission scenarios: SSP1-2.6 (best-case) and SSP5-8.5 (worst-case) across model calibration extents. Binary suitability used extent-specific MTSS thresholds.