Multiscale Ecological Niche Modeling Exhibits Varying Climate Change Impacts on Habitat Suitability of Madrean Pine-Oak Forests

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Anthropogenic climate change and increasing greenhouse gas emissions are expected to globally impact the biological function, community structure, and spatial distribution of biodiversity. Many existing studies explore the effect of climate change on biodiversity, generally at a single spatial scale. This study explores the potential effects of climate change on the habitat suitability of seven tree species at two distinct spatial scales: the Coronado National Forest (CNF), a local management area, and the Sierra Madre Occidental (SMO), an ecoregional extent. Habitat suitability was determined by extrapolating Ecological Niche Models based on citizen-science tree occurrence records into future climatic conditions using projected 30-year normals for two anthropogenic emissions scenarios through the end of the century. The results show that habitat suitability is expected to decrease for all seven tree species at varying degrees. Results also show that climate-forcing scenario choice appears to be far less important for understanding changes in species habitat suitability than the spatial scale of modeling extent. Additionally, we observed non-linear changes in tree species habitat suitability within the SMO and CNF dependent on forest community type, latitude, and elevational gradient. The paper concludes with a discussion of the necessary steps to verify the estimated shifts of these tree species under climate change. Most importantly, provides a framework for characterizing habitat suitability across spatial scales.

Contribution to the field

Our original research examines several topics for those modeling species distributions under current and predicted climates derived from anthropogenic emissions scenarios. With a focus on multiscale modeling, we examine the effects of anthropogenic climate change under two scenarios at the local and regional scale for seven tree species. We also examine how species may respond to climate across an elevation gradient, expert opinion locations of forest communities, and latitude. Results show that habitat suitability is expected to decrease for all seven tree species at varying degrees. Results also show that climate-forcing scenario choice appears to be far less important for understanding changes in species habitat suitability than the spatial scale of modeling extent. Our proposed framework and conclusions address the issues of spatial scale selection and provide future research a baseline in measurable tests to assess modeled shifts in species habitat suitability under climate change.

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Multiscale Ecological Niche Modeling Exhibits Varying Climate Change Impacts on Habitat Suitability of Madrean Pine-Oak Trees

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12 **Abstract**

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14 impact the biological function, community structure, and spatial distribution of biodiversity. Many
15 existing studies explore the effect of climate change on biodiversity, generally at a single spatial
16 scale. This study explores the potential effects of climate change on the habitat suitability of seven
17 tree species at two distinct spatial scales: the Coronado National Forest (CNF), a local management
18 area, and the Sierra Madre Occidental (SMO), an ecoregional extent. Habitat suitability was
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24 suitability than the spatial scale of modeling extent. Additionally, we observed non-linear changes in
25 tree species habitat suitability within the SMO and CNF dependent on forest community type,
26 latitude, and elevational gradient. The paper concludes with a discussion of the necessary steps to
27 verify the estimated alters of these tree species under climate change. Most importantly, provides a
28 framework for characterizing habitat suitability across spatial scales.

1 Introduction

30 Observed changes in Earth's physical and biological systems are directly related to the forcings of
31 anthropogenic climate change (Rosenzweig et al., 2008;Hansen and Stone, 2016). Increasing
32 greenhouse gas concentrations are expected to impact the world's climate through rising
33 temperatures, prolonged drought, and increasing contrasts between wet and dry seasons (Yanahan
34 and Moore, 2019). These human-driven alterations are negatively impacting biodiversity globally
35 (Kannan and James, 2009). These observed impacts include the progressive decoupling of species

36   interactions (i.e., plants and pollinators), extinctions of local populations along range boundaries, and
37   the extension of species geographic range boundaries towards the poles or higher elevations (Hughes,
38   2000). Due to global-scale impacts of anthropogenic climate change, it is likely that all species may
39   encounter varying alterations to their livelihood, habitat, and geographic range limits.

40   For biodiversity occupying sensitive habitats (i.e., mountains), climate change poses a significant
41   threat to species physiology, distribution, and community structure (Hao et al., 2007;Draper et al.,
42   2019). Montane plants and plant communities, referred to as the sentinels of climate change
43   (Malanson et al., 2019), often respond sooner to environmental changes than other species and
44   communities. Temperature increases caused by climate change are more significant at higher
45   elevation (Pepin et al., 2015), and species climate-induced range alters appear to be more sensitive to
46   elevation than latitude (Chen et al., 2011). While some species perish, others survive by in situ
47   adaptation or relocation to a higher or lower elevation (Colwell and Rangel, 2009). This observation
48   varies among species as the ability of a species to survive environmental change is determined by
49   their specific biological traits.

50   Traits such as propagule production and dispersal, post-fire regeneration, and shade intolerance drive
51   the relative ability to out-compete other species in any given location (Alexander et al., 2018) In
52   montane habitats, low elevation species that are adapted to hot and dry climates may out-compete
53   high-elevation species that are less suited for increased temperatures and aridity (Huntley, 1991;Chen
54   et al., 2011). Substantial range shifts upward in elevation as a response to climate change have been
55   identified in mountain environments throughout the world (Gottfried et al., 2012;Brusca et al.,
56   2013;Steinbauer et al., 2022). This trend may lead to decreased suitable habitat for high elevation
57   plant species and communities and increase competition as lower-elevation species move upward.
58   These communities may become increasingly fragmented as small, resilient patches of remnant
59   vegetation and become stranded among new vegetative communities (Coe et al., 2012;Yanahan and
60   Moore, 2019).

61   There are numerous studies, often model based, that examine how species distributions are altering
62   due to climatic change (Morin and Thuiller, 2009;Elith et al., 2010;Iverson and McKenzie, 2013).
63   Following suit, this study employs modeling to examine how tree species respond to anthropogenic
64   climate change using newly developed global climate change models forecasting through the end of
65   the century (Karger et al., 2017). Additionally, this study explores environmental change across two
66   spatial scales: Local and Regional. First, the local scale is represented by the geographic boundaries
67   of the Coronado National Forest (CNF), a topographically and ecologically complex management
68   area. While occupying a smaller geographic extent than is considered in most modeling-based
69   research (Kannan and James, 2009;Sousa-Silva et al., 2014), the CNF is a highly-managed forest,
70   and forest-wide proper characterizations of habitat suitability of tree species may assist land
71   managers in planning for potential climatic conditions such as drought, disturbance, and ecological
72   change. A smaller-scale study area also allows for more detailed explorations of other factors often
73   overlooked in large-scale studies. For example, preliminary reports suggest that local topography can
74   affect microclimate more than elevation (Schwilk et al., 2016), which, granted, may be only
75   observable at a higher spatial resolution. This highlights a need for research that explores how trends
76   in species responses to climate change will apply and be adapted into the applied management of
77   smaller, local-scale entities.

78 However, local analysis of species response to climate change may exclude variables only observed
79 at the regional scale. While land managers of the CNF may focus primarily on the ecological
80 occurrences within the forest boundaries, ecological function rarely follows geopolitical boundaries.
81 Thus, in addition to examining species responses to anthropogenic climate change at the local scale,
82 we also examine responses at the regional scale. The CNF represents the northernmost limits of the
83 Sierra Madre Occidental (SMO), a mountain range that extends across the United States and Mexico,
84 comprising the Madrean archipelago and mountains of Sonora, Mexico. By incorporating a regional
85 scale for comparison, we develop a separate scenario and alternative evidence for alterations
86 observed or not observed at the local scale. Regional models have been commonly linked to their
87 larger counterparts, the continental and global scale (Gallien et al., 2012;Taucare-Ríos et al., 2016).

88 The primary objective of this study is to examine how anthropogenic climate change may alter the
89 spatial distribution and quality of suitable habitat for 7 common tree species (i.e., 4 pine, 3 oak) that
90 provide the general structure of Madrean Pine-Oak Woodlands found throughout the SMO and CNF.
91 To predict the geographic response of each dominant species to anthropogenic climate change, we
92 employ Ecological Niche Modeling (ENM), a spatially explicit modeling approach to identify
93 species habitat suitability across space using a mean ensemble of three commonly used machine
94 learning statistical models. We fit models with environmental variables that reflect current conditions
95 along with future projections of climate under two anthropogenic emissions scenarios, formulated in
96 30-year climate normals for three time periods (2040, 2070, 2100). These scenarios are based on
97 social analogs, that range from moderate to severe in greenhouse gas emissions.

98   Niche models are then developed for each tree species for the current (2022) conditions, along with
99   the three future climate conditions under the two emissions scenarios, at the two spatial scales of
100 interest: Local and Regional. One unique contribution of this paper is the exploration habitat
101 suitability change for each tree species across elevation and latitude within the CNF. To accomplish
102 this, we employ Generalized Additive Models (GAMs) that examine how species are specifically
103 responding to climatic change across the CNF elevational gradient. Given these procedures, we
104 anticipate that 1) habitat suitability will decrease in geographic range and in quality (characterized by
105 the maximum values of habitat suitability) for all species examined, in both climate change scenarios,
106 with a more extreme response in the severe emissions scenario, 2) that species Genre (i.e., Pinus vs.
107 Quercus) will influence species response to climate change, with Pinus species responding more
108 poorly than those of Quercus, as SMO pine productivity is observed to decrease while oak
109 productivity to increase in a changing climate (Alfaro Reyna et al., 2019), 3) that species habitat
110 suitability will be observed to alter out of their associated biological communities with both pine and
111 oak species occupying communities higher in elevation, 4) conforming with previous studies, that
112 species habitat suitability will alter to higher elevations, and 5) higher latitudes, and lastly 6) that
113 models produced at different spatial scales (local vs. regional) will behave differently due to the
114 varying environmental values captured in the SMO ecoregion, with regional model exhibiting greater
115 changes in elevation and latitude. Our results provide an important template for local-scale and
116 regional-scale explorations of climate-induced habitat suitability change and should assist land
117 managers who are anticipating the impacts of anthropogenic climate change.

118 **2. Materials and Methods**

119 *2.1 The Local and Regional Scale*

120   This study uniquely examines two separate spatial scales with the smaller scale being a subset of the
121   larger. This purpose serves to examine how species are predicted to respond to climate change based
122   on the extent and range of environmental variables you incorporate. The regional scale is represented
123   by the SMO (Figure 1.A.). The SMO is known for its high biological and cultural diversity and
124   enormous environmental and economic importance (González-Elizondo et al., 2013). At an
125   approximate 290,000 km^2, the SMO is home to a high diversity of flora, including 24 different
126   species of Pinus 54 species of Quercus, and many other trees species (Silva-Flores et al., 2014). Due
127   to such a large geographic range of forested land, the SMO presents challenges in the management of
128   species, and is often filtered down to distinct management zones.

129   The local-scale, CNF is in Southeastern Arizona and Southwestern New Mexico, USA and borders
130   northern Mexico (Figure 1.B.). With an area of approximately 7,200 km^2, CNF comprises 12
131   geographically distinct management areas across 16 isolated mountain ranges, often called the "Sky
132   Islands", that form the northernmost extent of the Madrean Archipelago. Located in the Sonoran
133   Desert, these ranges produce an orographic effect, creating cooler, wetter climatic conditions at
134   higher elevations that reach upwards of 3,267 meters above the surrounding desert floor (Figure 1).
135   These high elevation Sky Islands are biodiversity hotspots supporting over 7,000 floral and faunal
136   species with many plant and animal communities usually only seen in more northern latitudes
137   (Yanahan and Moore, 2019). The American Southwest climate, in which the CNF is located, is
138   predicted to increase in temperature by 5-8 degrees Fahrenheit (13-15 Celsius), decrease in
139   precipitation by 10%, and increase in the number and duration of periods of high temperature
140   (Service, 2013).The CNF presents unique and challenging opportunities for land managers and
141   climate change research due to abrupt variations in topographic variables (i.e., elevation, slope,
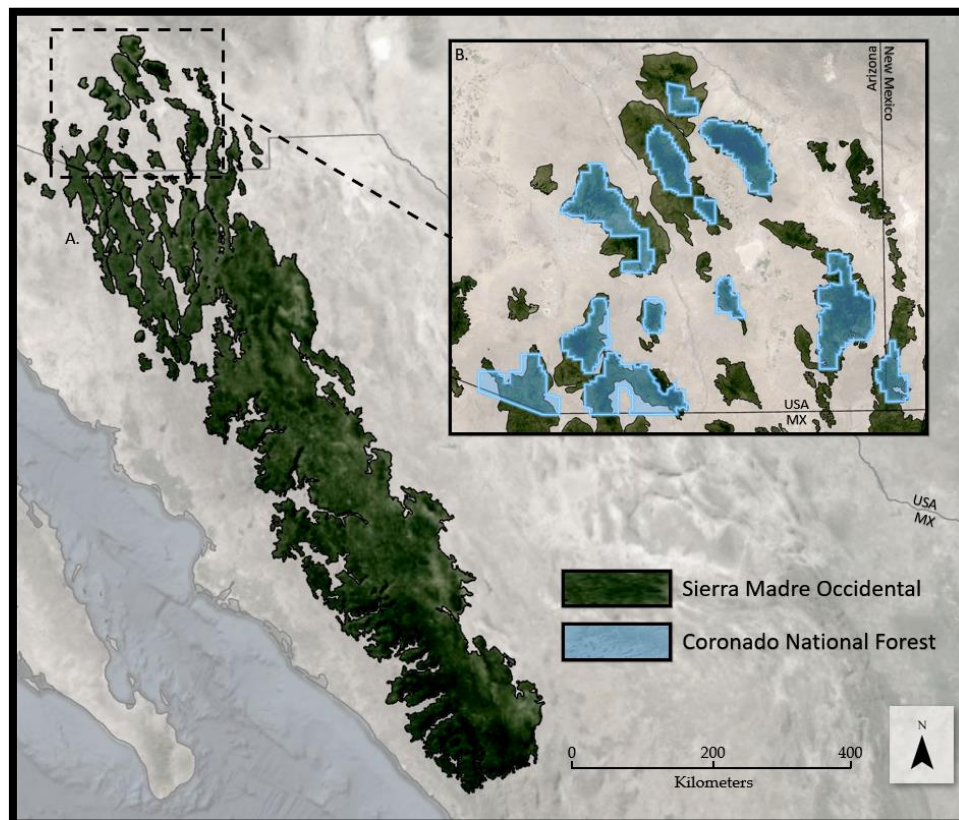142   aspect) and the isolation between mountain ranges.

143

144   **Figure 1.** The spatial extent of A. the Sierra Madre Occidental (SMO) symbolized in dark green and,
145   (B.) the Coronado National Forest boundary in light blue overlaid.

146   *2.2 Tree Species*

147   The highly variable climate across the elevational gradient of the SMO and CNF (Figure 2.A.) allows
148   for the development of distinct forest communities. These communities range from Broadleaf
149   Evergreen Oak woodlands at lower elevations to Spruce-Fir forests at high elevations. Forest
150   communities are distinct assemblages of trees at different successional stages or compositional
151   maturity (Davis, 1981). While somewhat variable in occurrence across the landscape, the SMO and
152   CNF houses major forest communities of interest (Service, 2013) (in general order of ascending
153   elevation): 1) Broadleaf Oak 2) Coniferous Woodland; 3) Coniferous Transition Forests; 4)
154   Coniferous Mixed Forests; 5) Engelmann Spruce-Alpine Fir Forests; and 6) Bristlecone Pine-Limber
155   Pine Forests. A portion of this study focuses primarily on the first four communities mentioned
156   (Figure 2.B.), with data provided from the United States Department of Agriculture (USDA) Forest
157   Service, Service Southwestern Region GIS Data (USDA Forest Service, 2022). Due to limited data
158   availability, the two highest elevation forest communities, Engelmann Spruce-Alpine Fir Forests and
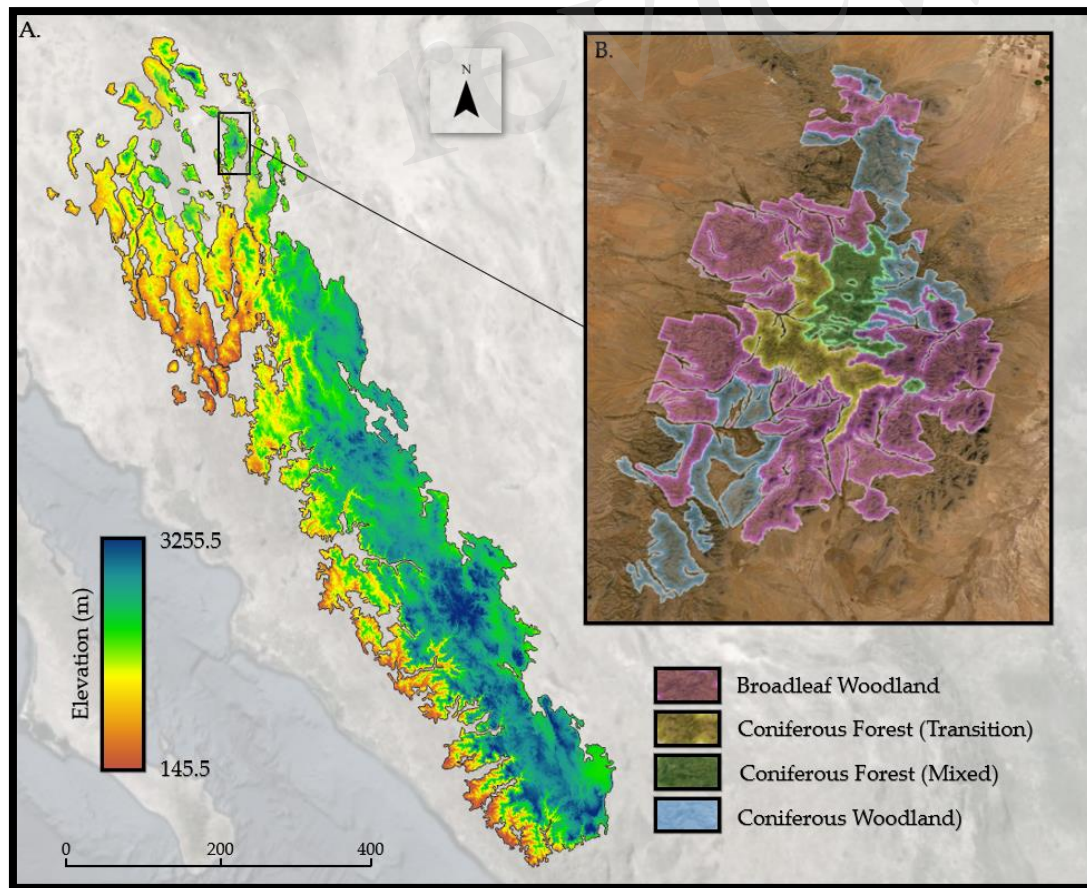159   Bristlecone Pine-Limber Pine Forests located in the Pinaleño range, were excluded from this study.

160

161   **Figure 2.** A. Elevation gradient for the spatial extent of the Sierra Madre Occidental and, B. Expert-
162   opinion spatial extents of the four forest communities of interest.

163 Ecological community composition may range from few to many species, resulting in a complex
164 system of species competing or relying on each other for resources. Forest communities, represented
165 by dominant, co-dominant, and understory (sub-canopy) plants, rely on the dominant species, whose
166 crowns commonly rise above the general canopy. Dominant trees provide various functions that
167 guide overall forest community function and structure (Power et al., 1996). Observations suggest that
168 dominant tree species direct the ecological processes that regulate microbial soil community
169 assembly, which play a critical role in maintaining forest functional and structural stability (Ma et al.,
170 2019). Dominant tree species are also driving factors in shaping spatial patterns of plant biodiversity,
171 locally and regionally (Hao et al., 2007;Draper et al., 2019). Examining the spatial distribution of
172 dominant tree species under climate change is a relatively new approach to understanding ecosystem
173 vulnerability, environmental change, and spatial conservation prioritization (Périé and de Blois,
174 2016;Wan et al., 2017;Dyderski et al., 2018). This study, while analogous to the overall topic,
175 uniquely examines the seven dominant tree species of the SMO and CNF (Table 1.).

176 **Table 1.** Scientific name, common name, and species code of the 7 tree species of interest. Table is
177 organized first by associated community then alphabetical order on scientific name. (=scientific
178 name) and (=code) represent the alternative names and codes of synonymous trees.

Scientific Name	Common Name	Code[1]
Quercus emoryi Torr.	Emory Oak	QUEM
Quercus arizonica	Arizona White Oak	QUAR
Quercus grisea	Gray Oak	QUGR3
Pinus leiophylla Schiede & Deppe	Chihuahuan Pine	PILE
Pinus engelmannii Carriere		PIEN2
(=*Pinus apacheca* Lemmon)	Apache Pine	(=PIAP)
(=*Pinus latifolia* Sarg.)		(=PILA5)
Pinus arizonica Engelm.	Arizona Pine	PIAR5
Pinus strobiformis Engelm.		PIST3
(=*Pinus ayacahuite* C.A. Ehrenb.)		(=PIAY)
(=*Pinus flexilis* James *var. reflexa* Engelm.)	Southwestern White Pine	(=PIFLR2)
(=*Pinus reflexa* (Engelm.) Engelm.)		(PIRE6)

179 [1] Species codes refers to recognized abbreviations for species. Codes were acquired from the United
180 States Department of Agriculture (USDA) National Resources Conservation Service (NRCS) Plant
181 Database (https://plants.usda.gov/).

182 *2.4 Climate Data*

183 The primary focus of this study is to examine how species' habitat distributions may change under
184 future climate change scenarios. We employed the use of 19 bioclimatic variables (Table 2),
185 commonly used in climate modeling research (Priti et al., 2016;Booth, 2018), produced from two
186 distinct future anthropogenic emissions scenarios from the Coupled Model Intercomparison Project 6
187 (CMIP6) (Karger D.N., 2018;Hamed et al., 2022), primary data modeling developed by the
188 Geophysical Fluid Dynamics Laboratory (GFDL), downscaled to a 1-km^2 spatial resolution by the
189 Climatologies at high resolution for the earth's land surface areas (CHELSA) research (Karger et al.,
190 2017). The two scenarios, known as Shared Socioeconomic Pathway (SSP) 3-7.0 and SSP 5-8.5, are
191 sectioned into three distinct 30-year normals: 2040 (2011-2040), 2070 (2041-2070), and 2100 (2071-
192 2100). Each SSP, derived from anthropogenic emission scenarios, ranges from moderate to extreme
193 climatic change through the end of the century (Alizadeh et al., 2022). SSP 3-7.0 infers that future
194 global climate results in the medium to the high end of the range of future forcing pathways, leading
195 to exceptionally high aerosol emissions and land use change (Meinshausen et al., 2020). SSP 5-8.5,
196 while similar in overall trajectory, represents the high end of the range of future pathways with a
197 reference scenario in a high fossil fuel development world throughout the 21st century (Meinshausen
198 et al., 2020). While more than two scenarios exist, data availability and the feasibility of SSP 3-7.0
199 and SSP 5-8.5 becoming a reality drove selection over other available SSP used in this study. Thus,
200 we developed seven Ecological Niche Models that use the 19 bioclimatic variables associated with a
201 specific time frame (Current, 2040, 2070, 2100) and SSP (3-7.0 and 5-8.5).

202 **Table 2.** Name and commonly used abbreviation for the 19 bioclimatic variables used in this study
203 for historical and future climate.

Bioclimatic Variable Name	Abbreviation
Annual Mean Temperature	BIO1
Mean Diurnal Range	BIO2
Isothermality	BIO3
Temperature Seasonality	BIO4
Maximum Temperature of the Warmest Month	BIO5
Minimum Temperature of the Coldest Month	BIO6
Temperature Annual Range	BIO7
Mean Temperature of the Wettest Quarter	BIO8
Mean Temperature of the Driest Quarter	BIO9
Mean Temperature of the Warmest Quarter	BIO10

Mean Temperature of the Coldest Quarter	BIO11
Annual Precipitation	BIO12
Precipitation of Wettest Month	BIO13
Precipitation of Driest Month	BIO14
Precipitation Seasonality	BIO15
Precipitation of Wettest Quarter	BIO16
Precipitation of Driest Quarter	BIO17
Precipitation of Warmest Quarter	BIO18
Precipitation of Coldest Quarter	BIO19

204

205   *2.3 Ecological Niche Modeling*

206   Ecological Niche Modeling (ENM), synonymous with Species Distribution Modeling (SDM) and
207   Habitat Suitability Modeling (HSM), is the process of relating geographically referenced species
208   occurrence records (i.e., presence/absence records), environmental variables (i.e., elevation, soil
209   moisture, annual mean temperature, etc.), and using statistical algorithms to predict habitat suitability
210   for a given species across a region of interest (Pearson, 2007;Elith and Franklin, 2013). ENM is
211   commonly applied to studies researching the consequences of future climatic change on the
212   geographic distribution of species (Nakao et al., 2013;Moor et al., 2015). Our study uses ENM to
213   investigate the geographic alterations in suitable habitat of tree species of the SMO and CNF under
214   various anthropogenic climate change emissions scenarios (Figure 3.). In ENM, no one model is
215   constituted as "best". Therefore, we implemented a mean ensemble approach from three machine
216   learning algorithms commonly applied in ENM. These models include: 1) Random Forest (Breiman,
217   2001); 2) Maximum Entropy (Elith et al., 2011); 3) Boosted Regression Trees (De'Ath, 2007).
218   Models were fit with 38 species-specific climatic, topographic, and edaphic variables that reflect
219   common drivers of plant distribution as well as species presence data gathered from commonly used
220   citizen-science databases (e.g., Inaturalist (Matheson, 2014), Global Biodiversity Information Facility
221   (Robertson et al., 2014), 'USGSs' Biodiversity Information Serving Our Nation (Guala, 2019), etc.)
222   obtained through the Interface to Species Data Sources (spocc) R package (Chamberlain, 2021). The
223   use of species occurrence records collected through citizen-science methodology has been applied to
224   a number of ecological modeling studies and is observed to improve ENM accuracy (Amano et al.,
225   2016;Milanesi et al., 2020;Feldman et al., 2021;Matutini et al., 2021). Species pseudo-absences are
226   generated at a 2-1 ratio for every observed presence in the dataset through random sampling of points
227   across the modeling domain of the SMO and CNF, consistent with other pseudo-absence generated
228   studies (Barbet-Massin et al., 2012;Liu et al., 2019). Through the examination of presence and
229   pseudo-absence point data, classification of suitable habitat is identified through the relationship of

230 the environmental variables and produced as a probability from 0 to 1 that directly relates to habitat
231 suitability.

232 Given that three different models were used and have different conditions and modes of prediction, a
233 maximum kappa classification threshold was implemented for consistency across statistical algorithm
234 selection (Duan et al., 2014). Accuracy was measured using the Area Under the Curve (AUC),
235 Sensitivity, Specificity, and the True Skill Statistic (TSS). These metrics measure the ability of the
236 models to correctly classify the presence and pseudo-absences in the training data. Each mean
237 ensemble model predicts on the [0,1] interval that represents the estimated probability of species
238 occurrence (i.e., habitat suitability). Predictions are produced in a spatially explicit raster at a 1-km2
239 spatial resolution. Each species distribution and habitat model use current and projected 30-year
240 normals (Current, 2040, 2070, 2100) for the 19 bioclimatic variables under two scenarios (3-7.0 and
241 5-8.5) for the creation of 7 total model outputs for each species. Topographic and Edaphic variable
242 data remained consistent across all models regardless of scenario or time as this is beyond the scope
243 of this climate change-based study and projected changes in topographic and edaphic variables across
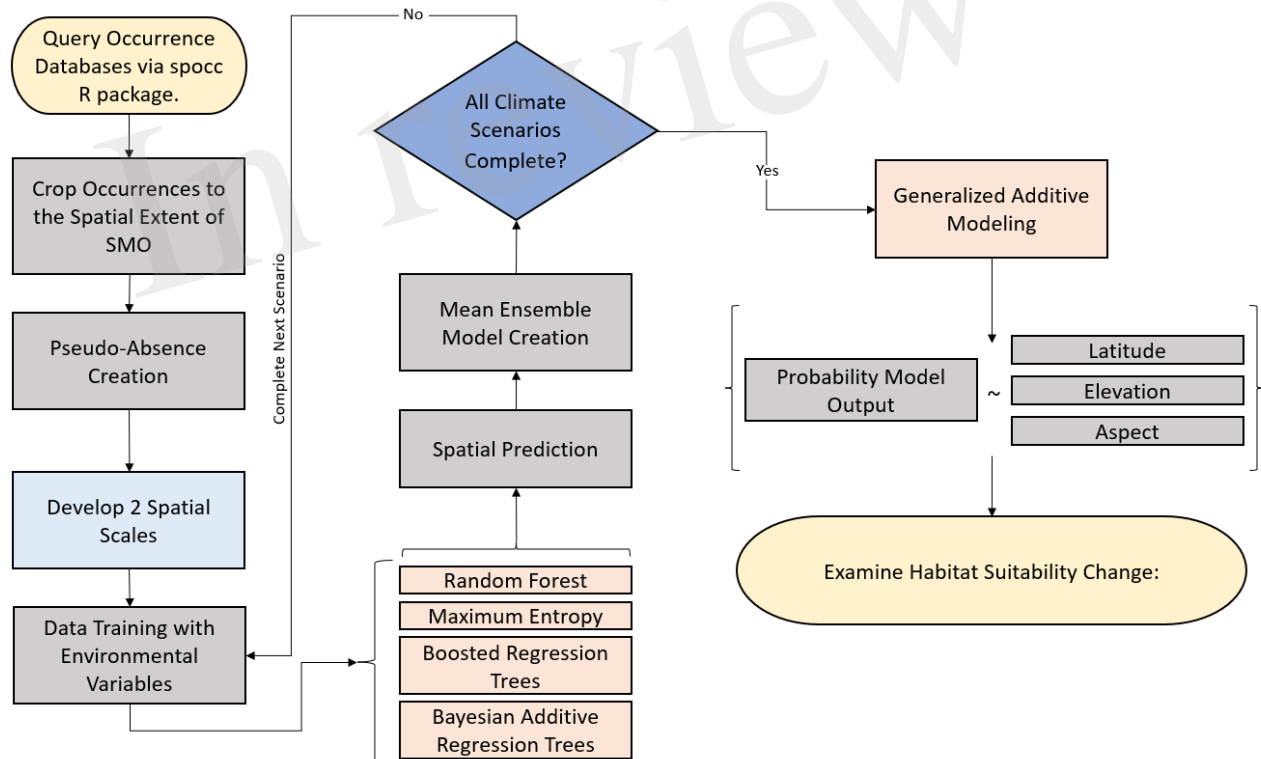244 time are largely unavailable.

245

246 **Figure 3.** Methodology flow-chart.

247 *2.5 Generalized Additive Models (GAMs)*

248 As previously mentioned, habitat suitability was estimated using an ensemble of three machine
249 learning algorithms at a 1 km^2 resolution at a local and regional scale. Post-ENM modeling, we
250 examined both models in their current extent, and clipped both models to the geographic boundaries
251 of the CNF (Figure 1.A.) This process allows for the examination of local vs. regional scale models
252 at 2 different scales and the examination of local vs. regional models when observed at the same
253 scale. A shapefile of the plant communities of interest (Figure 2.B.) (USDA Forest Service, 2022),

254 was used to partition the model grid cells into the distinct geographic boundaries of expertly defined
255 plant communities. Grid membership in the partition was based on the geographic coordinates of the
256 grid centroid. A GAM was used to relate the gridded estimates of habitat suitability to a gridded map
257 of elevation and latitude obtained from a 1km^2 digital elevation model of North America (Portal,
258 2007) and a shapefile of latitude from (ESRI, 2011).The gridded elevation and latitude maps was
259 resampled using bilinear interpolation to produce co-located elevation values for the grid of
260 suitability predictions. In this study, the GAM includes only a single predictor:

261 $$\hat{y} = \alpha + s(x)$$

262 where $\hat{y}$ represents the estimate of habitat suitability, x represents elevation, and α represents a
263 global model intercept (Hastie et al., 2009). The function $s(x)$ represents a smoothing spline, which
264 is a series of polynomial curves connected at breakpoints (often called "knots") in the x dimension.
265 The piecewise polynomials are required to be connected in such a way that the overall curve is both
266 continuous and differentiable. The number of knots in the spline determines how much local
267 variability is characterized: too many knots and the GAM will overfit the data, too few knots and the
268 GAM will smooth over the true relationship between x and y. In the R implementation smoothing
269 splines, the model smoothness is automatically selected by means of a penalized cross validation
270 (Wood, 2004;Wood, 2017). It is the authors' experience using the default smoothing settings in many
271 different contexts that the automatic smoothness selection rarely overfits the input data, especially
272 when the sample size of inputs is large ($n > 100$).

273 The assumptions made by the GAM model are that the data vary smoothly (though no model form
274 need be specified), and that the variance of the data about the true model form is constant. The
275 satisfaction of these assumptions allows for the estimate of prediction intervals as in ordinary least
276 squares (OLS) regression. The key difference between OLS and GAM modeling is that the GAM
277 does not require pre-specifying the model form that describes the relationship between x and y. This
278 allows great flexibility in determining smoothed representations of saturated scatterplots without
279 having to guess a model form a-priori. The popularity of GAMs for visualizing trends is evident in
280 the default smoothing options of R's most popular data visualization package ggplot2 (Wickham et
281 al., 2016).

282 **3. Results**

283 *3.1 Ecological Niche Models*

284 Habitat suitability for seven common tree species (Table 1.) was modeled using three machine
285 learning algorithms commonly applied in ENM for current climatic conditions and 2 future
286 anthropogenic emissions scenarios across 3 distinct 30-year averages. Mean ensemble models were
287 generated from the spatial outputs of the four algorithms for each of the seven scenarios. Common
288 modeling metrics (AUC, Sensitivity, Specificity, TSS) were generated producing the following
289 values for all models developed within the CNF domain (reported as median, mean): AUC (0.97,
290 0.98), Sensitivity (0.93, 0.94), Specificity (0.95, 0.91), and TSS (0.86, 0.85). Values for all models
291 developed within the SMO domain are as follows: AUC (0.96, 0.95), Sensitivity (0.88, 0.84),
292 Specificity (0.96, 0.88), and TSS (0.82, 0.72). Statistically, models performed consistent with the
293 standards of modeling accuracies and analogous research (Marmion et al., 2009;Williams et al.,
294 2009). With AUC mean values above 0.90, it is inferred that the models have high predictive

295 capability according to the predictor and response variables provided. Metrics for each specific
296 model are found in the appendix (Table S1.).

297 *3.2 End of Century Observations*

298 Habitat suitability is observed to alter in both spatial distribution and quality (i.e., overall modeled
299 probability) for all 7 tree species of interest, regardless of emissions scenario (Figure 4.). For pine
300 species, habitat suitability is observed to be negatively impacted by anthropogenic climate change in
301 both quality and spatial distribution across the entire SMO extent. Pinus engelmannii (PIEN), is
302 observed to be most negatively affected among the pine species. PIEN models produced a maximum
303 probability prediction of 98% under current conditions with high values above 81% in both southern
304 and northern extents of the SMO (Figure 4.2.A). Under the predicted emission scenarios of SPP 3-7.0
305 and SSP 5-8.5 for the year 2100, PIEN is predicted to decrease significantly, ranging in maximum
306 probability of 61% (SPP 3-7.0) and 56% (SSP 5-8.5) (Figure 4.2.B – Figure 4.2.C). The other 3 pine
307 species exhibit characteristics that are complex to describe spatially. Pinus leiophylla (PILE) is
308 observed to decrease in habitat suitability across the SMO over time but retain more pixels than
309 others that could be interpreted as moderate suitability at 41%-60% (Figure 4.3). Pinus arizonica
310 (PIAR) (Figure 4.1) and Pinus strobiformis (PIST) (Figure 4.4) are observed to have more pixels that
311 could be interpreted as low suitability (0%-40%). However, PIAR and PIST contain pixel values that
312 reach a maximum probability of 79% and 81%, respectively, ranging from 9%-11% greater than the
313 highest pixel predicted for PILE (70%).

314 Oak species are predicted to fare much better than pine species, in terms of both habitat quality and
315 spatial distribution within the extent of the SMO. The highest predicted probability value of oak
316 species was those reported from Quercus arizonica (QUAR) models (Figure 4.5) for current and end-
317 of-century conditions for both scenarios, which ranged from 96% to 93% to 94%, respectively.
318 Quercus emoryi (QUEM) (Figure 4.6) and Quercus grisea (QUGR) (Figure 4.7), exhibit decreases in
319 maximum probability prediction in both future scenarios to a greater, but not extreme extent than
320 QUAR, with values ranging from 95%-89% (QUEM) and 94%-88% (QUGR). Increased suitability is
321 observed for all oak species in more southernly extents of the SMO in future scenarios. Among these,
322 QUEM may show the greatest increase in habitat suitability across the SMO in terms of habitat
323 suitability, spatial exhibiting pixels to increase from a reported 0%-40% suitability (Figure 4.6.A) to
324 greater than 80% (Figure 4.6.B and Figure 4.6.C).

325 When compared visually, emission scenario shows little variation on the predicted habitat suitability
326 of species at the end of the century. Models reported contrasting, yet to be considered insignificant,
327 maximum probability predictions for each species in SSP 3-7.0 and SSP 5-8.5. For example, PIAR
328 shows a maximum probability of 79% at the end of the century for both future scenarios. The other 3
329 pines show slight decrease of 61% to 56% (PIEN), 71% to 70% (PILE), and 82% to 81% (PIST) for
330 SSP 3-7.0 and SSP 5-8.5, respectively. With exception of QUAR, which reports a higher maximum
331 probability in SSP 5-8.5 (94%) than SSP 3-7.0 (93%), oaks follow suit with either constant or
332 decreasing values among emissions scenarios at a fixed 89% (QUEM) or 89% to 88% (QUGR).
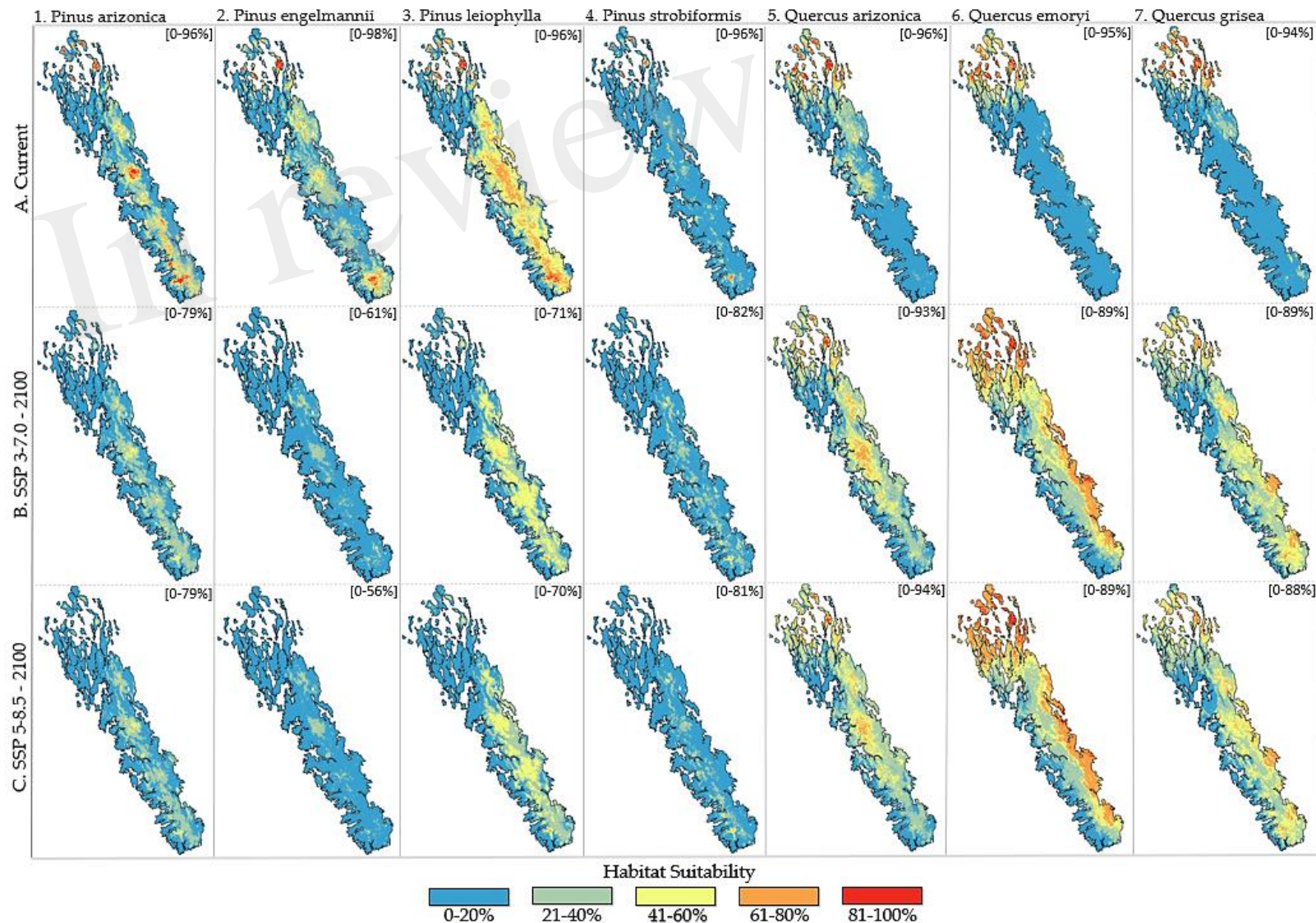
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Figure 4. Habitat suitability for the 7 tree species of interest across the Sierra Madre Occidental for current climatic conditions, end-of-century (2100) climatic conditions for SSP 3-7.0, and end-of-century (2100) climatic conditions for SSP 5-8.5. Habitat suitability probability is represented on a gradient of blue (low suitability) to red (high suitability). Predicted model probability range is in the upper right corner of each species map as [lower-upper%]. Figure column is assigned numerically while column is assigned alphabetically for rapid lookup (i.e., Pinus Strobiformis at end-of-century conditions for SSP 3-7.0 = Figure 4.4.B).

3.3 Spatial Scale Comparisons

A primary focus of this study was to not only observe species responses to anthropogenic climate change in terms of habitat suitability and spatial distribution, but to do so at both local and regional spatial scales. Model outputs were cropped to the boundaries of the CNF (i.e., local scale) and end-of-century predictions under SSP 5-8.5 (see Figure 5.) were compared. The magnitude of differences in predicted habitat suitability for each species across the two model scales varied greatly depending on species. Some species, such as PIEN, showed similar predictions for suitability in the CNF using the two modeling scales. Other species, like QUEM, showed differences in model predictions that were larger than the projected changes in suitability due to climate change. The general trend observed among pine species is a decrease in habitat suitability when comparing SMO and CNF modeling domains. Variation from this trend is observed in PIAR and PIST models as some areas are shown to increase in habitat suitability in the SMO modeling domain. Another observation among pine species is that the SMO modeling domain may result in a spatially focused prediction, with less values predicted at 41%-60% and more at 61%-80%. Consistent with previous observations in section 3.2 (*End of Century Observations*), PIEN shows very little habitat suitability while PILE shows consistent values for both modeling domains at the end of the century for SSP 5-8.5.
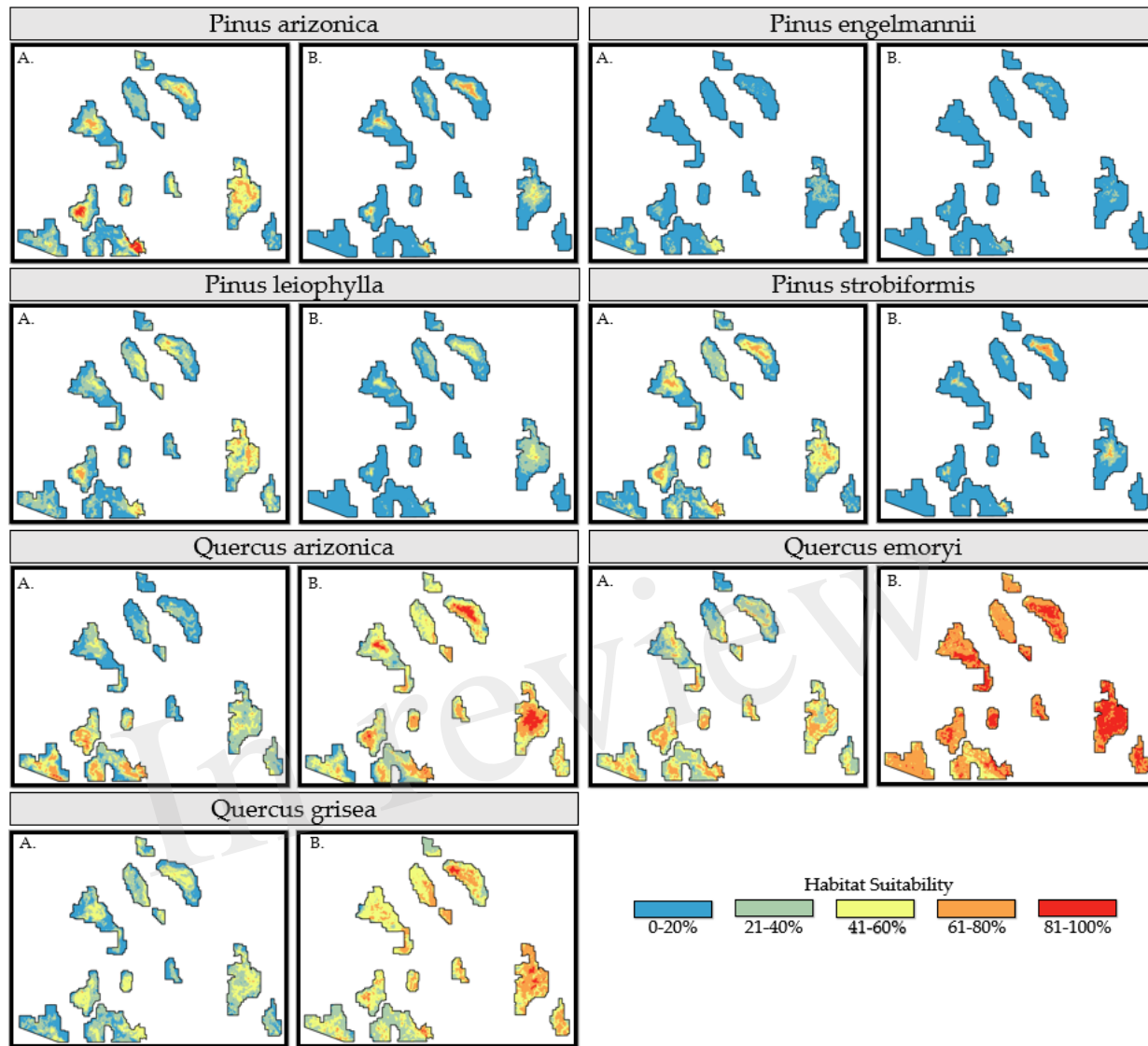
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Figure 5. Habitat suitability models of all 7 tree species of interest under the SPP 5-8.5 emissions
scenario for 2100. Each species model is cropped to the boundary of the Coronado National Forest
under two distinct modeling scales: A. Coronado National Forest and, B. Sierra Madre Occidental.

Oak species show more consistency as compared to pine species among observed predictions in both
modeling domains when compared to Section 3.2. Both modeling domains show higher estimates of
habitat suitability when compared to most pine species, however, there are arguably more significant
variations in predicted habitat suitability when comparing the two modeling domains. All three oak
species visually show increased values predicted in habitat suitability in SMO modeling domains
than CNF modeling domains. QUEM, when cropped to the SMO modeling domain shows no pixels
reporting values below 41%, with a large portion reporting greater than 61%. QUAR shows increases
in the northern ranges of the CNF with values ranging from an observed 0%-40% in CNF modeling
domains to greater than 41% with most pixels reporting 81% and above in SMO modeling domains.
Regardless of specific pixel value being reported, visually, there is significant difference in the
comparison between model outputs produced from the CNF modeling domain and SMO modeling
domain.

370   *3.4 Forest Community Suitability*

371   Estimated mean suitability within each community for each of the seven species is shown by points,
372   while whiskers represent the interquartile range (Figure 6). Note that the whiskers provide a sense of
373   the variability in estimated suitability across communities but do not provide any insight into the
374   variability of the estimated suitability within individual grid cells (i.e., no information on the random
375   forest prediction variance). Figure 6. shows variation in habitat suitability for each species across
376   communities, except for QUEM models at the SMO modeling domain extent, which report similar
377   values across all communities in future scenarios. The most notable observation is the decreasing
378   values in habitat suitability across time for all species, except for QUEM, which reports slight
379   increase over time. Perhaps equally interesting is the lack of variation among modeling domains for
380   the pine species in estimated suitability across time. When examining modeling domain, Oak species
381   show quite significant variation in reported habitat suitability for all communities across time, with
382   the SMO modeling domain estimating much higher suitability than the CNF. Additionally, pine
383   species show consistent higher prediction values in habitat suitability for forest communities that are
384   higher in elevation. Most interestingly, only one oak species (QUGR) follows the general trend
385   observed among the pine species. This may suggest that higher elevations are becoming increasingly
386   important for pine species survival, and QUAR and QUEM may be potential invaders to higher
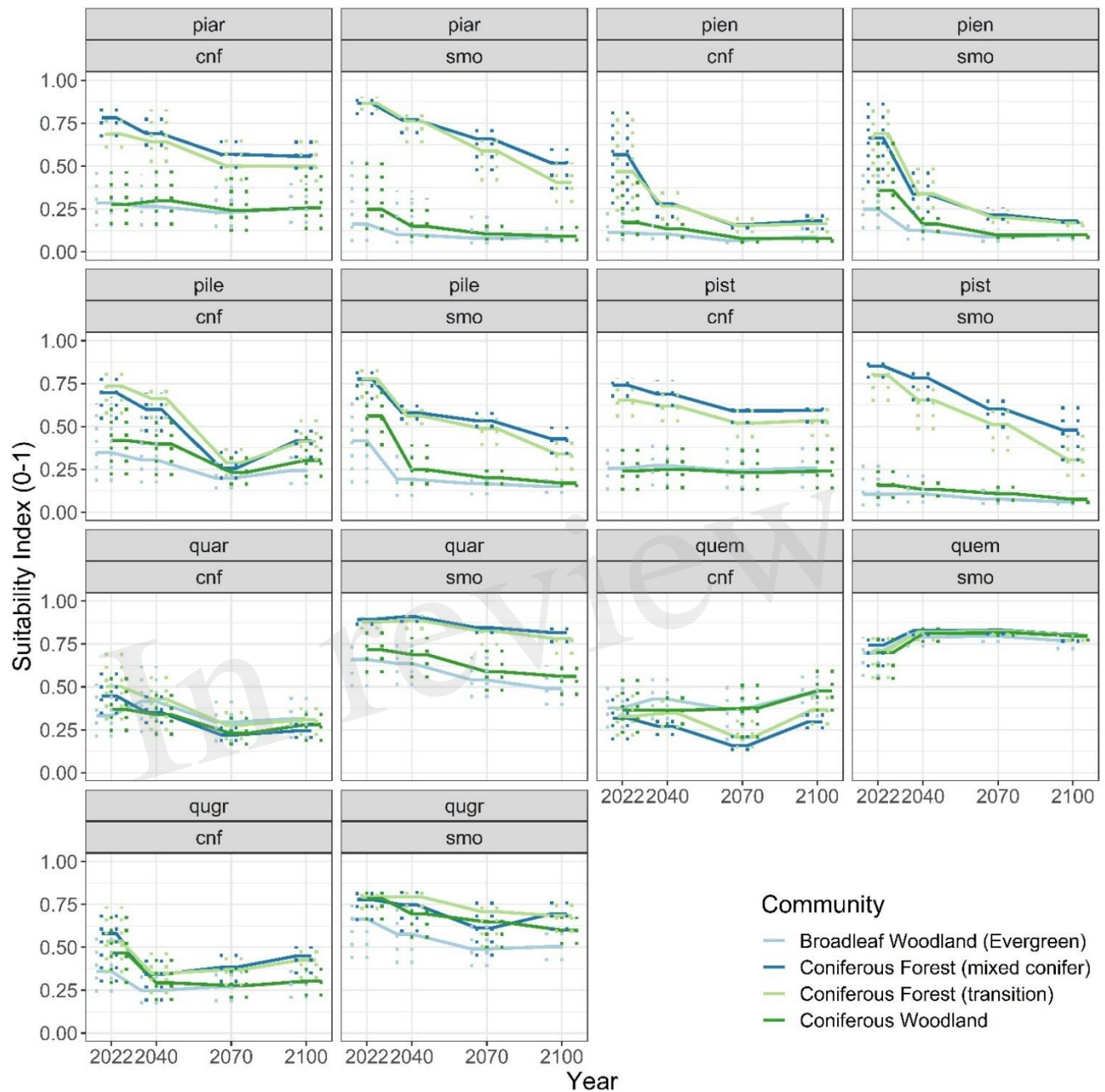387   elevation forest communities.

388

Figure 6: Projected change in habitat suitability of the seven tree species of interest within four common forest community boundary designations in the Coronado National Forest. Lines represent the mean estimated suitability within community, while the whiskers show the interquartile range of suitability within each community.

3.4 Suitability and Elevation

The two most natural characterizations of habitat suitability are over space and time. However, elevation drives climate variability over small geographical distances like the CNF (Randin et al., 2009). Figure 7. shows smoothed estimates of mean habitat suitability for all seven species across elevation within the CNF boundaries. Black, solid lines indicate the model estimates of suitability for current climate conditions, while the colored, dashed lines indicate the estimates of suitability for the

399 end of the century under two emissions scenarios. In total, there were 8,139 gridded estimates of
400 suitability and elevation that fell within the national forest boundaries. Thus, Figure 7., contains three
401 GAM estimates per species across two modeling domains, each using 8,139 unique points that show
402 each species projected habitat suitability across elevation. GAM estimates across elevation allows us
403 to visualize species responses to anthropogenic climate change that are difficult to detect accurately
404 in mapping products like Figures 4 and 5. All pine species, are observed to show decreased habitat
405 suitability for elevations below approximately 2,700m, when compared to current conditions. Above
406 approximately 2,700m, all pines modeled to the extent of the SMO increase in habitat suitability,
407 while the same species modeled at the CNF extent do not. Pine species also show much higher level
408 of agreement among the estimates for different emissions scenarios within modeling extents than the
409 same emission scenarios across modeling extents.

410 GAM estimates of oak species suitability across elevation varies drastically depending on the species.
411 Most notably, models developed at the SMO modeling extent show higher suitability across all
412 elevation than those developed at the CNF modeling extent. The commonly highest values in habitat
413 suitability across elevation for pines were reported by current conditions while oaks report varying
414 results, with each species exhibiting a different emission scenario as the highest. Oaks also report a
415 dip in habitat suitability, at approximately 1,500m, which is most likely the result of combinations in
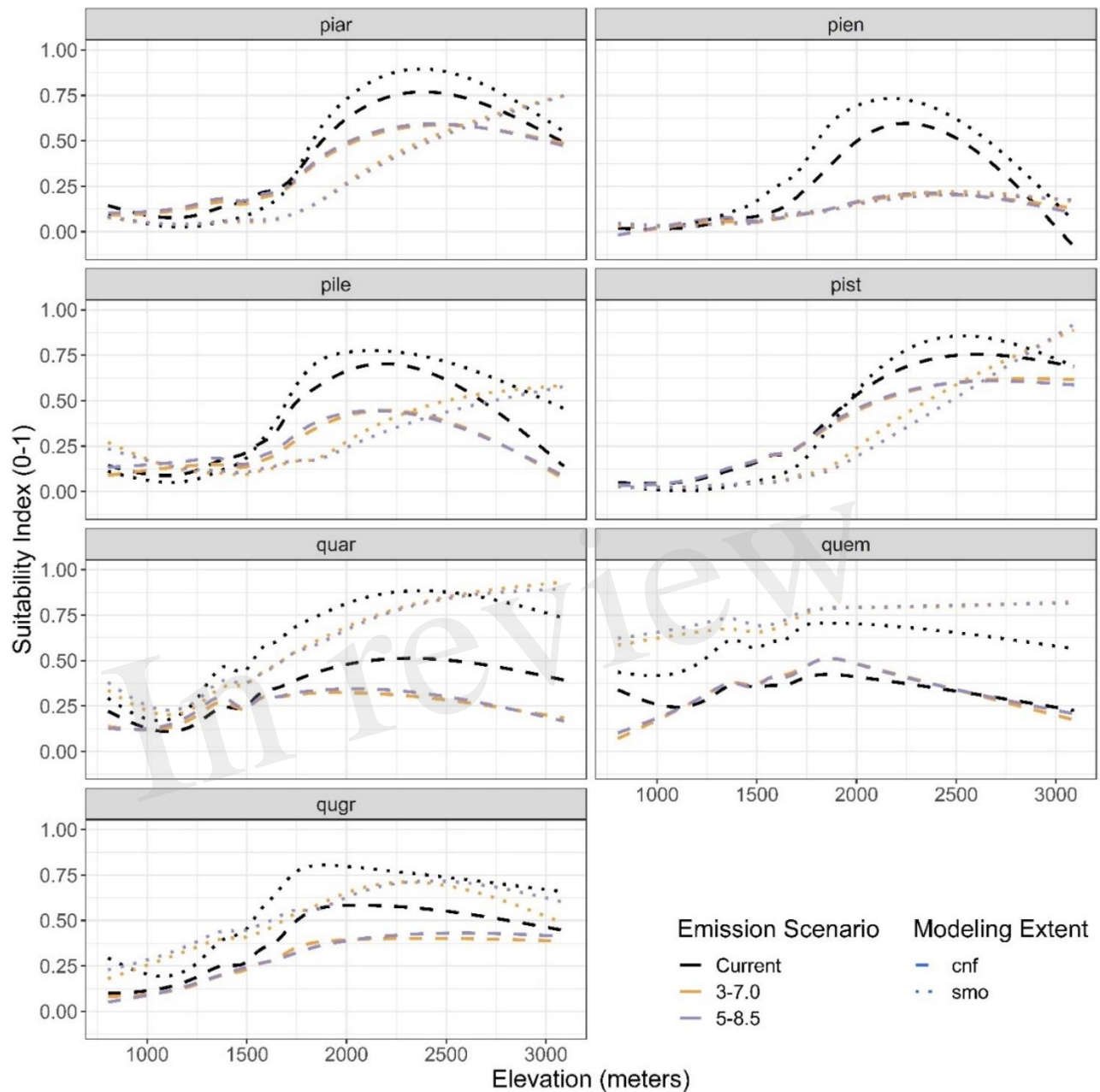416 available land for habitat at that elevation.

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Figure 7: Comparison of the smoothed relationship between mean habitat suitability and elevation
for the seven tree species of interest in the Coronado National Forest for current conditions (black,
solid) and 2100 estimates (colored, dashed) under different emissions scenarios. The shaded grey
regions indicate the 95% confidence interval of the GAM estimate of current suitability.

3.5 Suitability and Latitude

Figure 8. shows smoothed estimates of mean habitat suitability for all seven species across latitude
within the SMO. Black, solid lines indicate the model estimates of suitability for current climate
conditions, while the colored, dashed lines indicate the estimates of suitability for the end of the
century under two emissions scenarios. Latitude is observed to be a driving factor in species response
to a changing climate (Colwell et al., 2008) and represents and interesting variable to consider among
multiple-scale modeling comparisons. Arguably, latitude would play little role in species response to

429   climate change within the spatial extents of the CNF. The SMO, however, is a reasonably large
430   ecoregion spanning more than 10 degrees in latitude. Habitat suitability of pine species was similarly
431   reported to respond to climate change across latitude, with a small over decrease in suitability for
432   PIEN. Oak species show similar responses across latitudes with general increases in habitat
433   suitability under future emissions scenarios. Future emission scenarios for QUAR and QUGR
434   eventually taper off at cross with current conditions at high latitudes, while QUEM exhibits higher
435   values in habitat suitability across all latitudes. Interestingly all species respond to latitude greater
436   than 32 degrees with an abrupt increase. This is likely due to the patchiness and sharp increases in
437   elevation across space for mountain ranges occupying of the Madrean Archipelago and CNF.
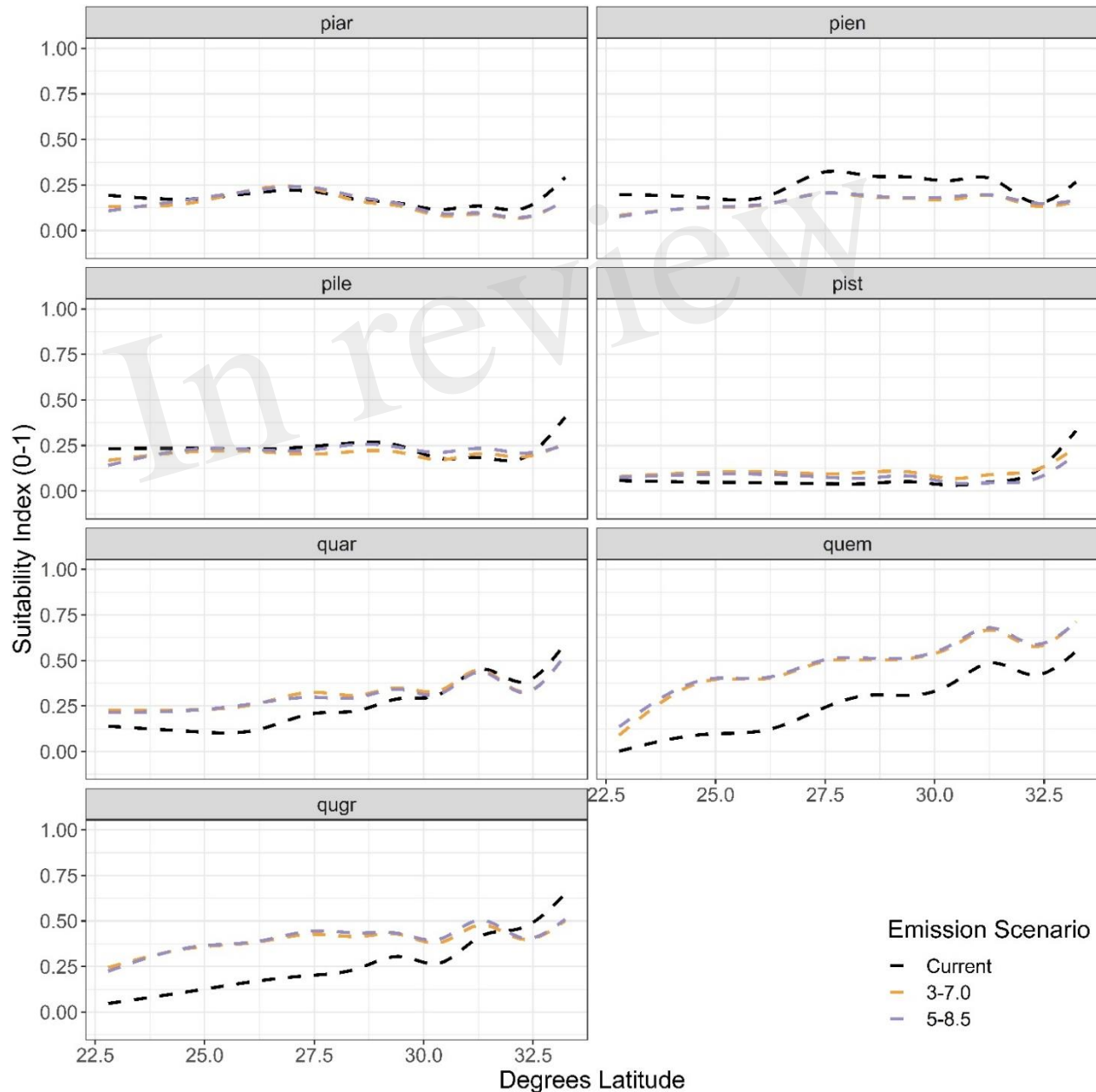
438

439   **Figure 8**: Comparison of the smoothed relationship between mean habitat suitability and latitude for
440   the seven tree species of interest in the Coronado National Forest for current conditions (black, solid)

441   and 2100 estimates (colored, dashed) under different emissions scenarios. The shaded grey regions
442   indicate the 95% confidence interval of the GAM estimate of current suitability.

443   **4. Discussion**

444   Our results indicate substantial alterations in habitat suitability among all tree species across all
445   emissions scenarios and spatial scales. Pine species habitat suitability is observed generally to
446   decrease in both spatial distribution and habitat quality. Changes in habitat suitability for is more
447   localizes and species specific. These results align with anticipated shifts in species distribution from
448   recent, analogous research (Du et al., 2021;Erfanian et al., 2021;Rödder et al., 2021). Our study also
449   suggests that when modeling species distributions under predicted anthropogenic emissions scenarios
450   at local and regional scales, climate forcing scenario choice appears to be far less important for
451   understanding drivers in species habitat suitability than the spatial scale of models. This claim
452   suggests that conservation efforts based on ENMs must consider and address their spatial scale of
453   choice, and where possible, consider the sensitivity of model results to varying spatial extents.
454   Ignoring options in the spatial extent at which models are used to train data overlooks the fact that all
455   model results are conditional on a somewhat arbitrary choice of modeling domain.

456   One shortcoming of the models developed at the CNF extent is that only occurrences of tree species
457   in a limited range of climates, which makes it difficult to know how species might behave in an
458   unobserved future climate. The SMO models overcome this shortcoming by providing a greater
459   range of climate model inputs, thus avoiding inappropriate model extrapolation. That in mind, the
460   SMO spans multiple countries with vastly different opinions of forest management. It this becomes
461   difficult to distinguish climate effects from geopolitical effects at the regional scale. This reinforces
462   the need for researchers to carefully consider the consequences of their spatial modeling extent
463   choice.

464   Modeling in general, has its weaknesses and shortcomings. The ENM techniques presented in this
465   study ignore the reality of biotic relationships and that species are in competition with each other for
466   limited resources (Fern et al., 2019). One goal addressed was to examine if a alterations among
467   species occupying a particular community (i.e., Broadleaf woodland, Coniferous Woodlands, etc.)
468   would invade the boundaries of another community. We did see this occur as examined in Figure 6.
469   However, each species occupying a community generally neighbors the spatial boundaries of other
470   plants. This means that even small changes in habitat suitability could lead to drastic and non-linear
471   changes in the competitive balance between species, resulting in large alterations in community
472   composition and distribution. Future studies would benefit from more direct investigations of the
473   change in the competition among species, rather than looking solely at the habitat suitability of
474   species individually.

475   Another consideration is a matter of spatial resolution. Small-scale variability is difficult to derive
476   from course-grained, global climate data. Additionally, substantial changes in species habitat
477   suitability projected in larger-scale studies may overlook small-scale areas like the CNF, which may
478   present resilience to certain aspects climate change. Local-specific features such as streams and
479   springs could influence micro-climate forest communities to be more or less resilient (Wieser et al.,
480   2003;Anderson et al., 2007). However, the smallest spatial resolution of climate data freely available
481   at the time of this study was 1 km^2, which would not capture fine-resolution microclimate. The
482   heterogeneity that occurs with scale highlights the need for spatial models to match the scale of

483   specific management boundaries (i.e., local, regional, global). This would allow models to be more
484   applicable to the immediate climate adaptation science and land stewardship efforts.

485   Additionally, differences between modeled distribution alterations and realized alterations may be the
486   result of tipping points generated by extreme events (Saccone et al., 2009;Niu et al., 2014). Alters in
487   typical climate conditions over a 30-year period may not be substantial enough to considerably
488   change habitat suitability while increases in the yearly variance may supply a sufficient threat in
489   forest resilience (Wang et al., 2016). For example, one exceptional drought could provide the catalyst
490   for widespread forest fires or insect outbreaks that would noticeably alter the ecology of the CNF.
491   Wildfires (expected to be more frequent and widespread in the future) could have large consequences
492   due to the different fire resilience and post-fire rejuvenation of each species (Barton and Poulos,
493   2018). Additionally, our results imply significant changes in species habitat suitability across
494   elevational, community, and latitudinal gradients, but realized changes in species distributions may
495   be a result of temporal lags individual response to climate change. Our study reinforces the point that
496   modeling efforts may allow us to anticipate the future, but ultimately should be used in conjunction
497   with observations in current and stochastic environmental occurrences.

498   Modeling the future is an exciting topic in the field of landscape ecology and management, however
499   the true consequences of anthropogenic climate change will be realized in observation over time. The
500   results of this study call for the long-term monitoring of forest species. Our models, reliant on geo-
501   referenced species presence largely collected by citizen science, allows land managers to develop a
502   more-focused resampling and ground-truthing program, to continually update and add to the
503   reliability of habitat models. We also suggest a distinct monitoring of seedlings and seedling habitat
504   suitability, presents a significant role in forest change over time as tree regeneration is the driving
505   factor in long-term survival (Ribbens et al., 1994). Additionally, we suggest that when considering
506   the use of ENM for applied conservation efforts, to do so at multiple scales. Doing so will allow for
507   1) the capture of a greater range of influencing environmental drivers on species habitat suitability
508   and, 2) a greater confidence in model result and interpretation. Opportunities abound in the
509   application of ENM to multiple spatial scales of interest as local, complex study areas like the CNF
510   may misrepresent changes only observable at the regional scale, which in an era of global
511   environmental change, may be costly to management and potentially fatal to biodiversity.

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523 **Data Availability Statement:** The data presented in this study are available by request, or by digital
524 download at: https://www.hydroshare.org/resource/070cd1b6e2d64aab9704af6f0b3b4d16/

538 **Conflicts of Interest:** The authors declare no conflict of interest.

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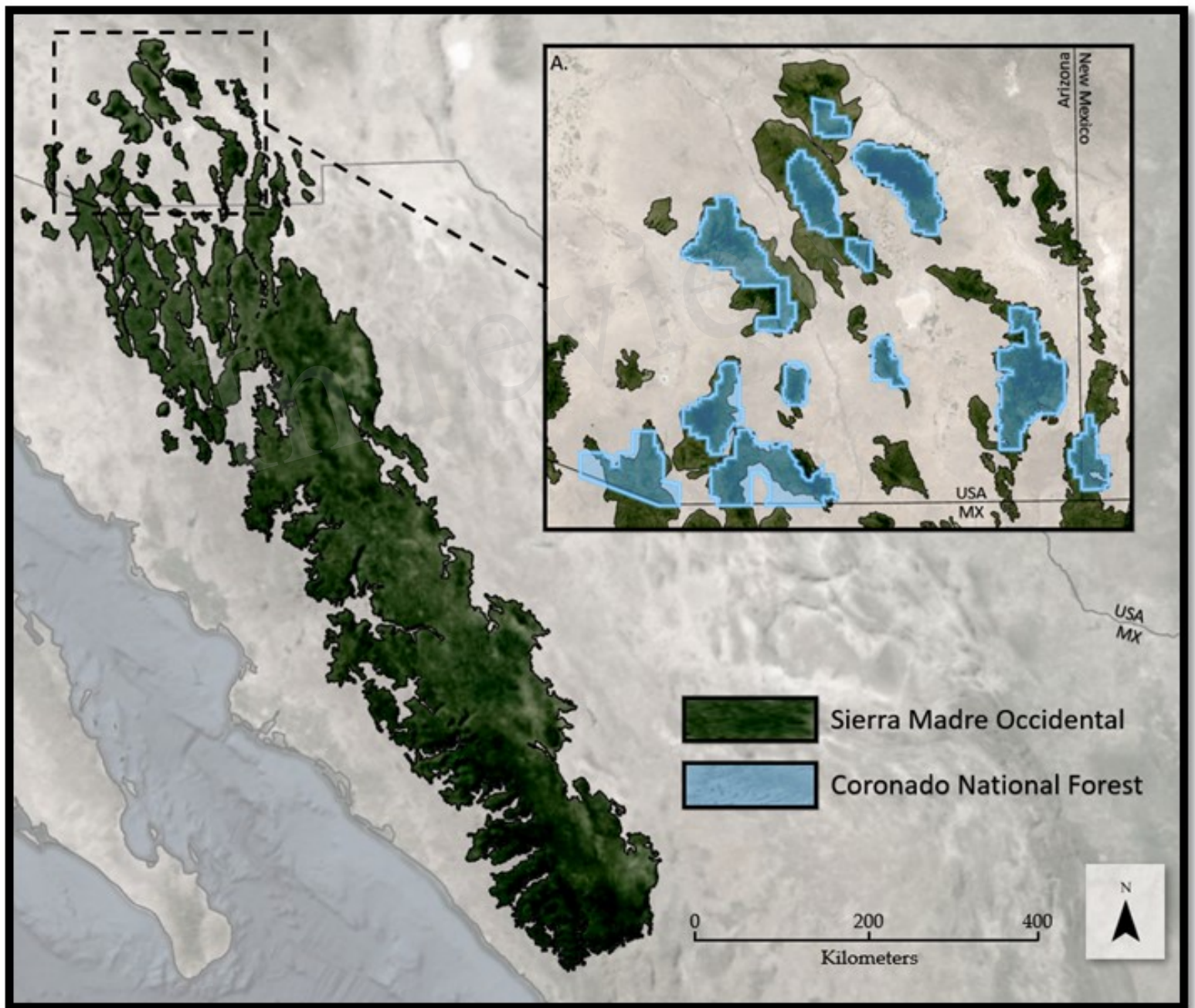768   Madrean Sky Island Archipelago. *Diversity and Distributions* 25.
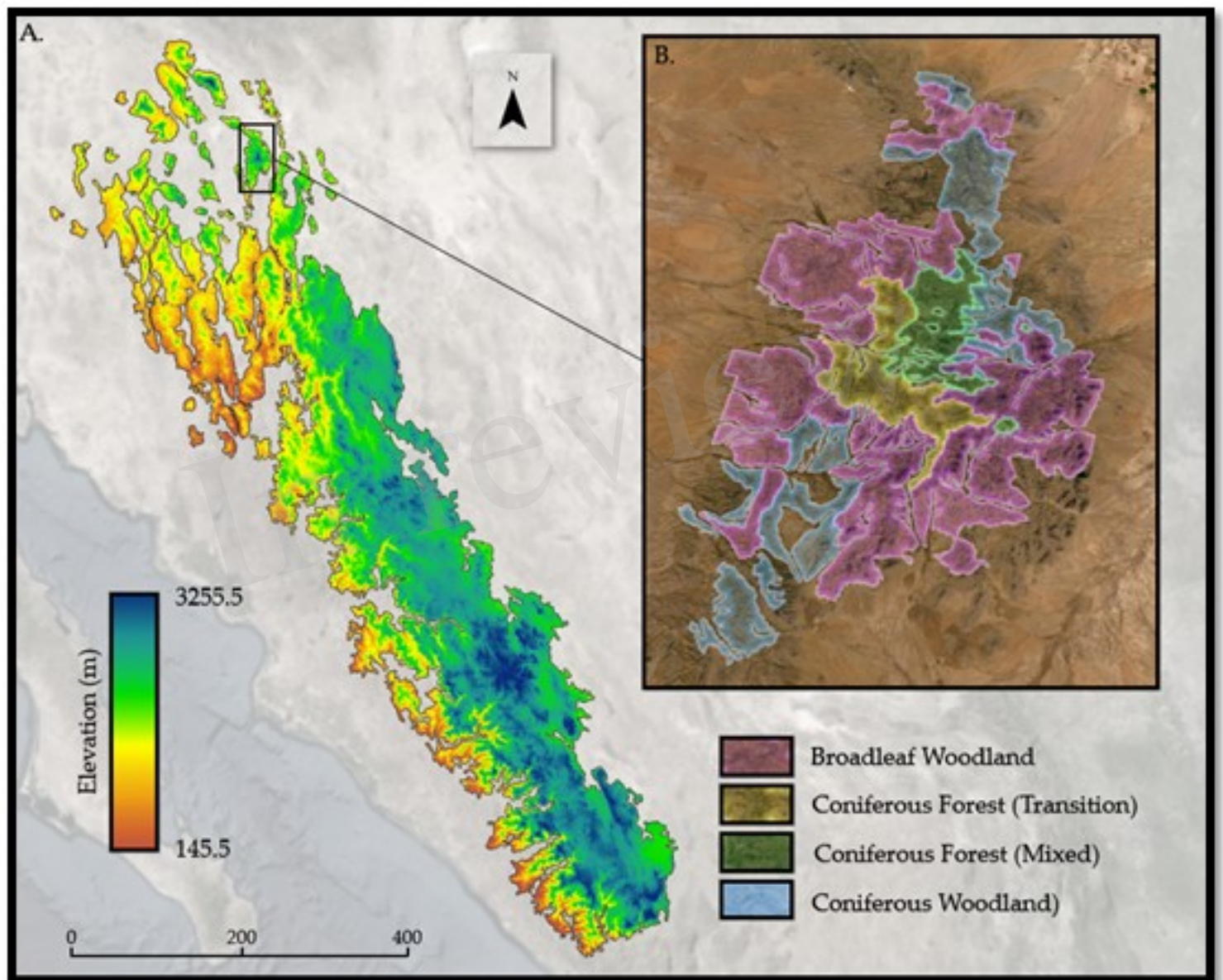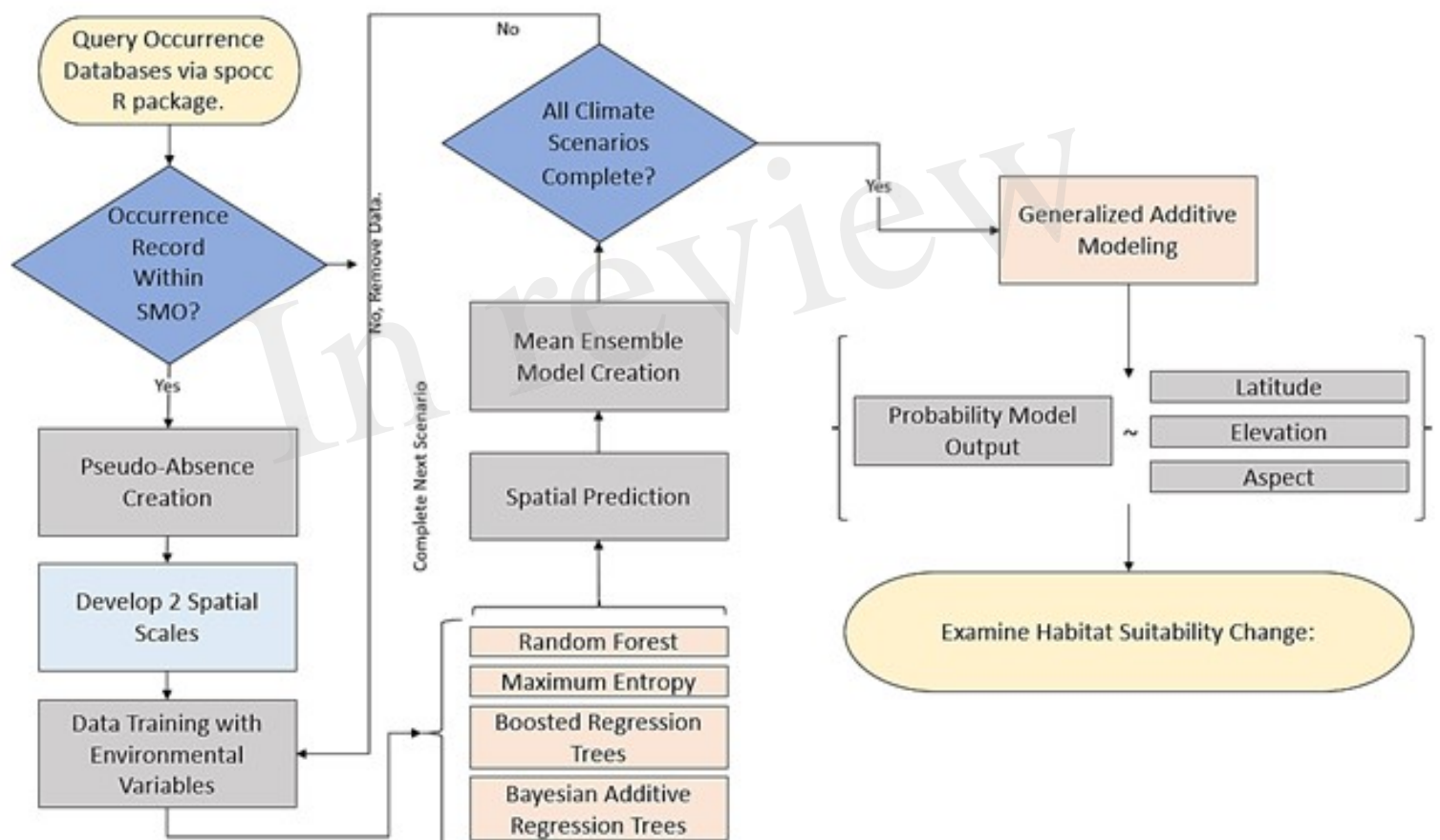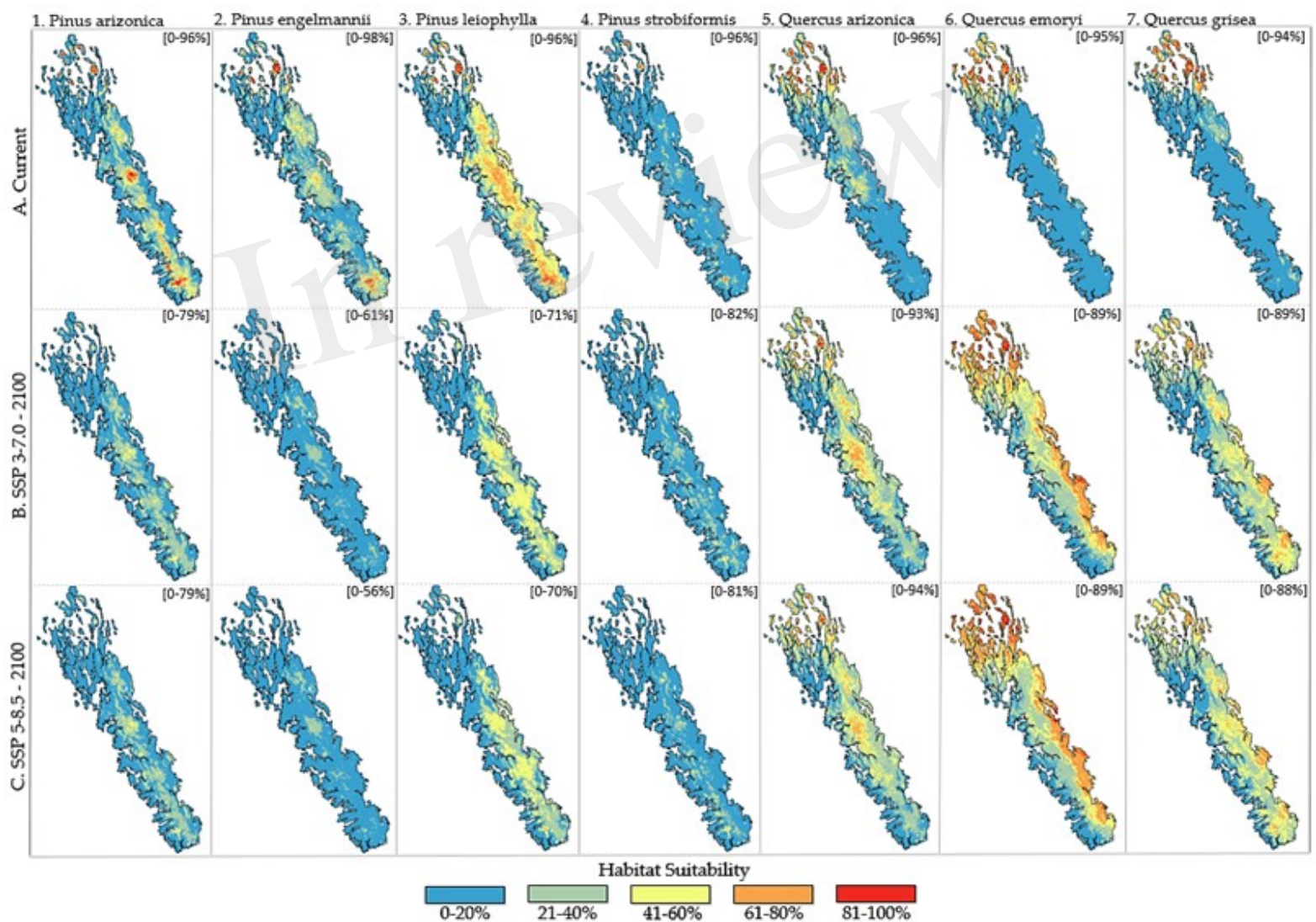
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Figure 1.JPEG

Figure 2.JPEG

Figure 3.JPEG

Figure 4.JPEG

Habitat Suitability

0-20%   21-40%   41-60%   61-80%   81-100%
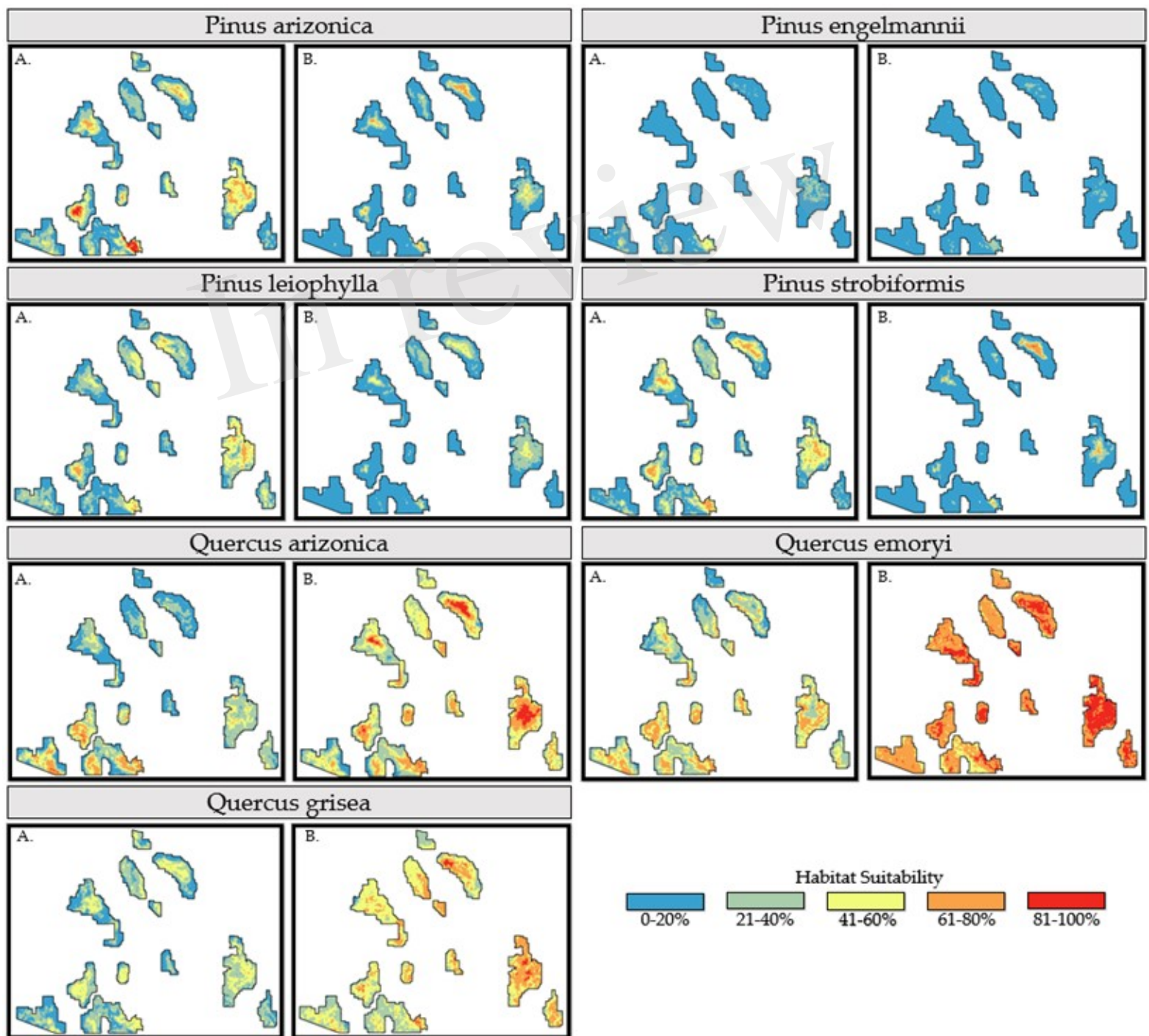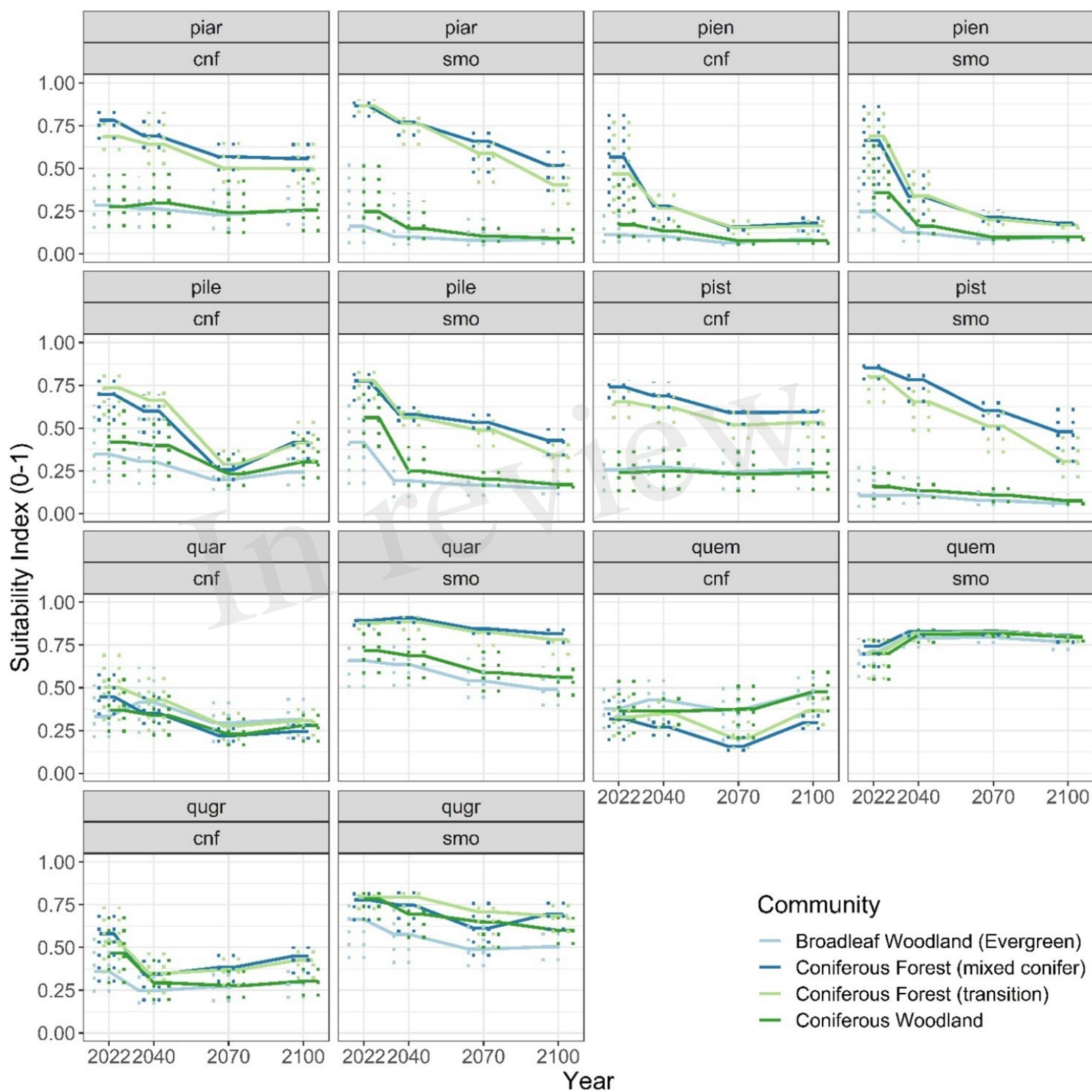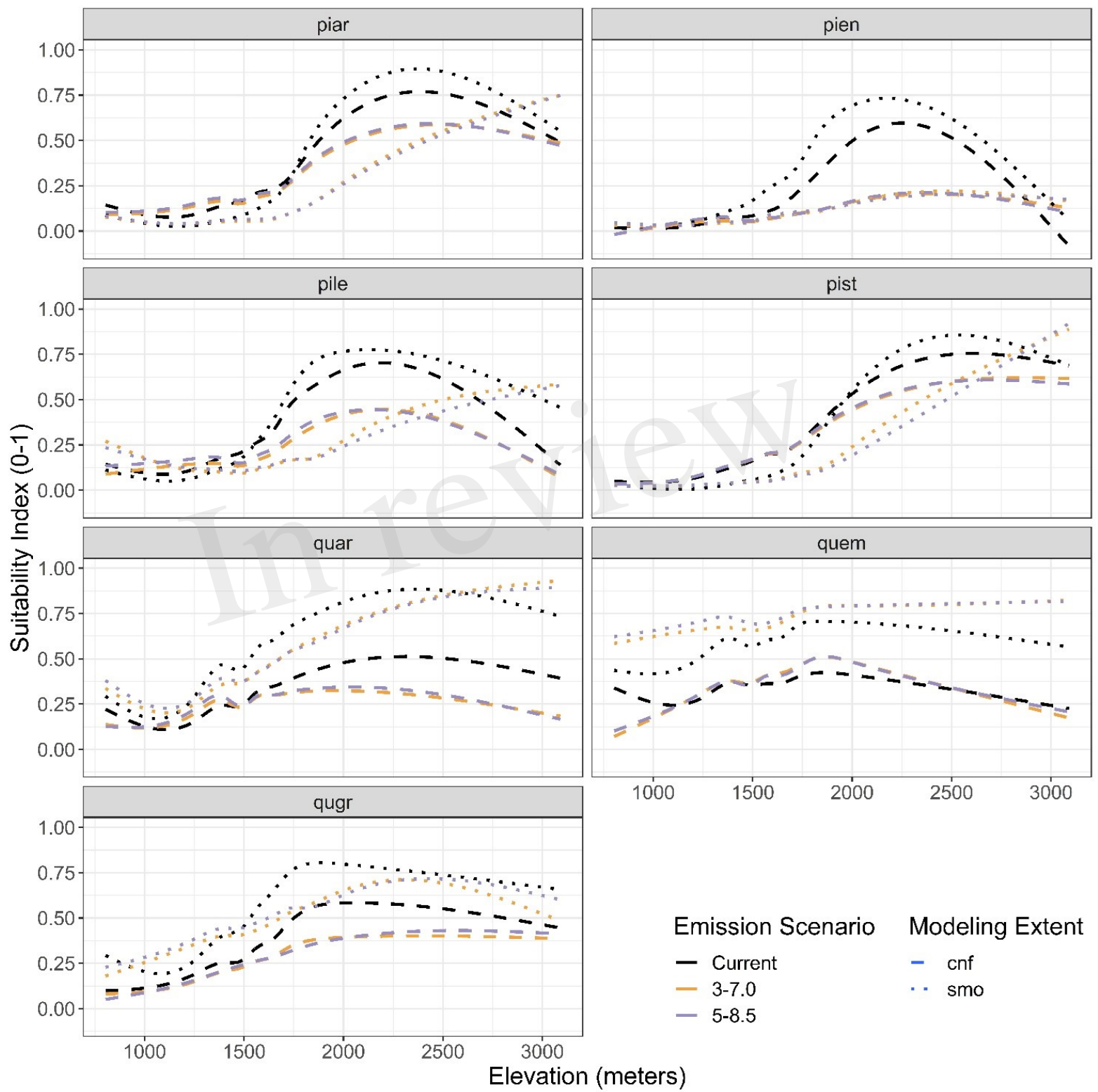
Figure 5.JPEG

Habitat Suitability: 0-20%, 21-40%, 41-60%, 61-80%, 81-100%

Figure 6.JPEG

Figure 7.JPEG

Figure 8.JPEG