Global Ecology and Biogeography

Climate change can exacerbate ant invasion impacts by unleashing indoor populations into outdoor environments

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Climate change can exacerbate ant invasion impacts by unleashing indoor populations into outdoor environments

Running title: Warming facilitates the spread of indoor ants

1 **Abstract**

2 Aim: While thousands of non-native species have established populations in outdoor

3 environments globally, many also have populations confined within indoor settings. Here,

4 we examine the general but rarely tested assumption that populations of non-native

5 species are confined to indoor environments when climatic conditions outdoors prove

6 inhospitable. We also investigate how climate change may influence the spread of indoor

7 populations into outdoor environments, and evaluate the capacities of different countries

8 to manage these potential invasions.

9 Location: Global.

10 Time period: Present.

11 Major taxa studied: Ants.

12 Methods: Leveraging a global dataset of ant species distributions compromising ~2.5

13 million occurrences, we modelled how regional climatic conditions and the native

14 climatic niche of each non-native ant species determine whether they are restricted

15 indoors. We then projected the model using current and future climatic conditions and

16 quantified the increase in outdoor non-native ant species in different regions under

17 warming. We further used a dataset of countries' invasive species management capacities

18 to evaluate whether the anticipated increase in outdoor non-native ant species would be

19 concentrated in countries with the highest management capacities.

20 Results: Non-native ants from warm environments are more likely to be restricted indoors

21 when introduced to cold environments. Importantly, additional climate warming may

22 relax restrictions on non-native ant species currently confined indoors, ultimately

23 contributing to a rise in outdoor non-native species richness, with the projected

24 increments averaging 2–3% and 8–9% across regions globally under 2°C and 4°C of

25 warming, respectively. The associated impacts are set to be highest in European countries

26 lacking comprehensive management and monitoring schemes.

27 Main conclusions: Our findings suggest that indoor environments serve as microclimatic

28 beachheads for biological invasions, especially in cold regions. Failure to limit climate

29 warming may facilitate the spread of indoor non-native populations into outdoor

30 environments, with costly repercussions on nature and society.

31

32 Keywords: Biological invasions, climate change, indoor pests, greenhouses, climate

33 matching, ants

34 **Introduction**

35 The recent IPBES assessment has identified biological invasion as a serious threat to

36 ecosystems, economic sectors, and human health globally (IPBSE, 2023). In the global

37 effort to understand and manage the impacts of biological invasions, numerous studies

38 have investigated the mechanisms determining the success of non-native species

39 establishments in outdoor environments (Abellán, Tella, Carrete, Cardador & Anadón,

40 2017; Bacon, Aebi, Calanca & Bacher, 2014; Dawson et al., 2017; Lockwood, Cassey &

41 Blackburn, 2005). In contrast, the factors influencing non-native species establishments

42 in indoor environments, such as buildings, stores, and greenhouses, have been

43 understudied. This is despite longstanding knowledge of the potential of indoor

44 environments to serve as invasion hotspots (Donisthorpe, 1927) ,and the fact that in some

45 regions, indoor environments contain as much as 71% of the total non-native species

46 richness of particular taxonomic groups (Kenis, Rabitsch, Auger-Rozenberg & Roques,

47 2007; Kobelt & Nentwig, 2008; Pergl et al., 2016; Roques et al., 2009; van Kleunen et

48 al., 2018). While many studies have highlighted how indoor environments can facilitate

49 the spread of non-native species to outdoor environments (i.e., where their impacts pose a

50 greater threat) (Hulme, 2017; van Kleunen et al., 2018; Wang, Zhang, Pan, Li & Zhu,

51 2015), these effects can be difficult to assess due to a lack of 1) comprehensive data on

52 non-native species residing indoors and 2) understanding of the mechanisms determining

53 the indoor and outdoor distributions of non-native species.

54   Increased similarities in the climatic conditions between the native distributions of

55 non-native species and their introduced regions is an important predictor of

56 establishment, known as climate matching (Richardson & Pyšek, 2012). It has been

57 suggested that indoor environments provide more suitable microclimatic conditions to

58 non-native species compared with outdoor environments (Hulme, 2017; Pergl et al.,

59 2016; Robinson, Martin, Loureiro, Matikinca & Robertson, 2020; Wang et al., 2015). If

60 climatic conditions are the primary drivers restricting non-native species indoors, climate

61 change can release indoor non-native populations into outdoor environments (Hulme,

62 2017; Robinson et al., 2020; van Kleunen et al., 2018; Wong, Economo & Guénard,

63 2023). This can subsequently amplify the burden of biological invasions on ecosystems

64 and societies, as some non-native species with indoor populations are known to generate

65 considerable environmental and socioeconomic impacts when established in outdoor

66 settings (Ahn, 1994; Cannon, Matthews & Collins, 2007; Cho, Kang & Lee, 2000;

67 Diagne et al., 2021). In such a scenario, a country's capacity to prevent and control

68 biological invasions ("response capacity" hereafter) will be vital in determining the

69 consequences of future invasions under climate change (Early et al., 2016; Faulkner,

70 Robertson & Wilson, 2020). An important but unaddressed question is whether the

71 anticipated spread of indoor non-native populations to outdoor environments with climate

72 change will concentrate in countries with high response capacities, such that these

73 emerging threats could be mitigated (Early et al., 2016; Faulkner et al., 2020).

74   Here, we use comprehensive distribution data of all known non-native ant species

75 (Guénard, Weiser, Gomez, Narula & Economo, 2017; Wong et al., 2023) to assess how

76 climatic conditions restrict their established populations to indoor environments globally.

77 In accordance with the climate matching hypothesis, we predicted that non-native ants

78 invading regions with similar climatic conditions to their native distributions would have

79 increased success in establishing outdoor populations. We further examined how climate

4

80   change would affect the distributions of indoor and outdoor populations of different non-

81   native ant species, and estimated the resultant changes in the number of non-native

82   species in outdoor environments across regions globally. Additionally, we examined how

83   the anticipated spread of non-native ants would potentially exacerbate their negative

84   environmental and socioeconomic impacts in regions globally. Finally, to examine

85   whether these potential invasions facilitated by climate change would be effectively

86   contained, we assessed the extent to which they were concentrated in countries with a

87   high response capacity to biological invasions.

88

Methods

90   **Data sources**

91   We leveraged information from four databases which are described briefly below (full

92   descriptions are provided in Supporting Information Text S1).

93   We obtained data on ant species occurrences from the Global Ant Biodiversity

94   Informatics (GABI) database, which contains nearly 2.5 million records of ant species

95   occurrences worldwide, extracted from the literature (~10,700 studies) and ant specimen

96   databases (Guénard et al., 2017). The database indicated whether regions belong to the

97   native and non-native range of each species. Regions were defined at country levels, or at

98   lower administrative units for larger countries such as China, Canada and the US. Several

99   regions—mainly those for island systems—reflected natural geographic boundaries

100   (Figure 1; see Text S1 for a complete description of the database). For each region, we

101   followed the hierarchical classifications of non-native ant species used in previous studies

102   (Wong et al., 2023), with "Indoor" referring to species with populations that were strictly

103   restricted to indoor environments, and "Naturalized" referring to species with populations

104   that had established outdoors. Records known only from quarantine facilities were

105   excluded. In total, the database identified 5,176 non-native populations of 373 non-native

106   ant species globally.

107   We obtained data on the environmental and socioeconomic impacts of non-native ant

108   species as impact scores from a recent global risk assessment of non-native ants (Gruber

109   et al., 2022). The database contained 1,162 impact records of 34 species from 642 studies.

110   We extracted the impact score of each ant species according to the Generic Impact Score

111   System (GISS), which was calculated based on six categories of environmental impacts

112   (e.g., "competition with other animal species") and six categories of socioeconomic (e.g.,

113   "crop loss") impacts.

114   We obtained data on current and future climatic conditions from TerraClimate, a

115   database of ~4 km resolution (Abatzoglou, Dobrowski, Parks & Hegewisch, 2018).

116   Specifically, we obtained data for the minimum temperature of the coldest month,

117   maximum temperature of the warmest month, total precipitation, soil moisture in both the

118   driest and wettest months, as well as the levels of seasonality in temperature,

119   precipitation, and soil moisture. We used the 2°C and 4°C warming scenarios for

120   subsequent model projections.

121   We obtained data on the response capacities of different countries to biological

122   invasions (Early et al., 2016) (Figure S1). The database scored the response capacities of

123   181 countries in 2015 based on their reports to the Convention of Biological Diversity

124 (https://www.cbd.int/reports). The scores of five categories were extracted, namely if 1)

125 countries recognized invasion threats, 2) a list of invasive species was available, 3)

126 management practices controlling invasive species existed, 4) there were research and

127 international collaborative programs to prevent or mitigate the impacts of invasive

128 species, and 5) invasive species was monitored. The scores of each category were either 0

129 ("No") / 1 ("Yes") or 0 ("None") / 0.5 ("Limited") / 1 ("Comprehensive"). A higher score

130 indicates that the given country had a higher capacity to mitigate the impacts of

131 biological invasions relative to other countries.

132   We acknowledge that countries' response capacities in 2015 may not reflect their

133 current response capacities. However, we used the available data to approximate the

134 relative differences in the response capacities between countries, rather than to estimate

135 the ability of each country to prevent invasions *per se* (Early et al. 2016). Studies have

136 shown that differences in socioeconomic conditions such as governance and education

137 levels can be important determinants of countries' response capacities (Latombe et al.,

138 2023). These socioeconomic conditions in 2015 and 2021/2022 (the most updated data)

139 exhibited strong positive correlations at country levels (Pearsons's r > 0.88) (Table S1,

140 Figure S2). Thus, the data should still reflect the relative differences in current response

141 capacities between countries.

142

143 **Modelling indoor status**

144   As the climatic variables were highly intercorrelated ($|R| > 0.7$), we ran separate PCAs

145 for the variables associated with temperature and those associated with water availability

146 and extracted the scores of PCA1 in each analysis. The scores of PCA1 explained 78%

147 and 63% of the global variation observed in climatic variables associated with

148 temperature and water availability, respectively. We did not retain the remaining PCA

149 axes because their explanatory power was not significantly higher than random, as

150 indicated by the broken-stick method in the R package BiodiversityR (Kindt, 2023).

151 Increasing temperature and water availability PCA1 scores indicate cooler, wetter, and

152 more seasonal environments (Table S1).

153   We first extracted PCA1 scores from each grid within the native distribution of each

154 species and averaged them to represent the climatic conditions in their native distribution.

155 We also obtained average PCA1 scores for each region in the introduced range. Finally,

156 we designated the timing of the earliest record of a non-native species within a region as

157 its introduction year, which would be used to proxy propagule pressure (Abellán et al.,

158 2017). We excluded populations that had no dated records (as we included the earliest

159 date of detection as a covariate in the model to proxy propagule pressure, see below), as

160 well as 14 species with no native distribution data available. These reduced the number of

161 non-native populations for subsequent analyses from 5,176 to 4,890.

162   As the response variable—the indoor status of each non-native species in each

163 region—was binary, we used mixed effects logistic regression to examine the effects of

164 different climatic variables. The model included records of all species from all regions,

165 and was built using the R package *glmmTMB* (Brooks et al., 2017). The predictors

166 included were the PCA1 of both the temperature and water variables in the introduced

167 and native range. In addition, we specified two two-way interaction terms in the model:

168   temperature PCA1 in the native distribution and the introduced region, and water PCA1

169   in the native distribution and the introduced region. Inclusions of interaction terms assess

170   how climatic conditions in introduced regions filter species based on their native

171   distributions (Miller, Damschen & Ives, 2019). We additionally included the introduction

172   year as a covariate to act as a control for propagule pressure (Abellán et al., 2017).

173   Introduction year was log-transformed to reduce skewness. We also used data on the

174   vertical habitat strata occupied by each non-native ant species (Wong et al., 2023), which

175   indicated whether a species was associated with different vertical habitat strata. In total,

176   species from six categories were analyzed ("litter-and-soil only", "ground only",

177   "arboreal only", "ground and litter-and-soil", "ground and arboreal", "all strata").

178   For the random effect structure, we first added polygon and species identity as random

179   intercepts. We also added climatic predictors as random slopes in the model to minimize

180   type-I and type-II errors (Harrison et al., 2018). In *glmmTMB*, the full model was

181   specified as

182   *Indoor.status~Native.Temp.PCA1*Introduced.Temp.PCA1+Native.Water.PCA1*Intro*

183   *dced.Water.PCA1+year+strata+(Introduced.Temp.PCA1+Introduced.Water.PCA1||spec*

184   *ies)+(Native.Temp.PCA1+Native.Water.PCA1||region)*

185   The full model, however, resulted in singularity fits. Thus, we excluded the

186   Introduced.Temp.PCA1 from the random effects (but not fixed effects), as its random-

187   effect variance was close to zero. After assessing the statistical significance of each term,

188   we excluded any insignificant interaction terms and reassessed the significance of the

189   main effects (Schielzeth, 2010). If these main effects were still insignificant, we removed

190   them from the final model before conducting climate change projections. We also used

191   the R package *DHARMa* (Hartig, 2022) to conduct spatial and phylogenetic

192   autocorrelation assessments. Phylogenetic autocorrelation assessments were based on a

193   genus-level phylogeny for ants (Economo, Narula, Friedman, Weiser & Guénard, 2018)

194   (Table S3).

195   The lack of indoor records in the tropics (Figure 1) could be driven by sampling biases

196   rather than ecological processes. Unfortunately, quantifying the extent of undersampling

197   in each region would be impossible. Thus, we used the number of indoor populations as

198   an indicator of undersampling, and assumed regions with 1) no indoor non-native

199   populations, 2) ≤ 1 indoor population, and 3) ≤ 2 indoor populations as "undersampled".

200   We then re-ran the best model based on these scenarios to ensure our results reflect

201   climatic effects but not sampling biases across climatic gradients.

202

Climate change projections

204   Future PCA1 scores were obtained for the introduced range, but not in the native

205   distribution, as we are primarily interested in climate change effects on driving future

206   invasions. Future PCA1 scores were based on extracting climatic variables from the 2°C

207   and 4°C warming scenarios and projecting them on the PCA1 axis obtained from current

208   climatic conditions.

209   We then projected the final model above using current and future climate conditions

210   for each introduced region in *glmmTMB* (Brooks et al., 2017). We calculated the effects

211   of climate change on each population as differences in their naturalization probability

212 between future and current climates. Our projections showed that naturalization

213 probability was at most reduced by 0.1% and 0.5% across all naturalized populations

214 under 2°C and 4°C warming scenarios (n=4,372). Thus, in subsequent analyses, we only

215 considered changes in the naturalization probability for indoor non-native populations

216 (n=512). We calculated the expected gain in naturalized non-native and harmful species

217 (Table S4) by summing the differences in naturalization probability between current and

218 future scenarios across all indoor non-native populations in each region.

219 To examine how the naturalization of indoor populations under climate change could

220 generate additional environmental and socioeconomic impacts in outdoor environments,

221 we calculated gains in cumulative impact scores of each region across all indoor harmful

222 populations between current and future climate scenarios. Specifically, the differences in

223 cumulative impact score in each region between future and current climate were

224 calculated as

$$\sum_{i=1}^{n}\sum_{j=1}^{6}(P_{i,Future} - P_{i,Current}) \times Score_{i,j}$$

225

226 where n was the number of harmful species with indoor populations, $P_{i,Future}$ and

227 $P_{i,Current}$ were the naturalization probability for species i under future and current

228 climate, and $Score_{i,j}$ was the impact score of species i in category j. Environmental and

229 socioeconomic impacts had six categories, thus the maximum number of j was 6. When

230 there were multiple scores available for the same impact category, we used the maximum

231 score for each species, a common approach in invasive species risk assessments (Gruber

232 et al., 2022).

233   Our analyses should not be interpreted as forecasts of the contributions of the spread

234   of non-native ants to the total impacts in different regions, as doing so would require

235   detailed data on how impacts vary across different environments. Instead, they aim to

236   identify the potential impacts that are often associated with indoor non-native ants

237   benefiting from climate change using impact scores. This approach is often used for

238   spatial risk assessment despite uncertainties in whether the potential impacts would be

239   realized, as a higher impact score indicates more potential impacts by non-native species,

240   justifying the prioritization of management (Bai, Chisholm, Sang & Dong, 2013;

241   Katsanevakis, Tempera & Teixeira, 2016).

242   To quantify the future increases of impacts relative to current impacts in outdoor

243   environments, we calculated the cumulative impact scores under current climate

244   conditions by summing impact scores across each naturalized harmful species in different

245   regions, with their naturalization probability set as one. We also calculated the sum of

246   gains in the cumulative impact score of each category across all regions under climate

247   change to better understand the primary mechanisms driving increased socioeconomic

248   and environmental impacts. Additionally, for each species, the cumulative changes in

249   environmental and socioeconomic impact scores across all indoor populations globally

250   were calculated separately to uncover which would be most responsible for increasing

251   future impacts.

252

Response capacity analyses

253

254   As the response capacity data was at the country levels (Figure S1), we upscaled the

255   regional impacts to minimize spatial mismatches. For instance, we aggregated data for all

256   states within the USA (except the minority of outlying islands). Briefly, we used the gain

257   in naturalization probability, environmental impacts, and socioeconomic impacts in the

258   worst-affected region to represent each country (see Text S2 for details).

259   To assess if the facilitated spread of indoor non-native populations to outdoor

260   environments by climate change would be restricted to countries with a high response

261   capacity, we obtained each country's total response capacity by summing scores across

262   the five categories. We then calculated the sum of gain in the naturalization probability of

263   non-native and harmful species, environmental impacts, and socioeconomic impacts

264   under climate change for each level of the total score. To identify the weakest aspects of

265   response capacity, we also assessed the proportion of highly threatened countries with

266   existing or comprehensive policies in different aspects. To ensure our results were not

267   sensitive to arbitrary thresholds, we assessed the response capacity of the top 10 and 20

268   countries with the highest projected gains in each metric and scenario.

269

Results

270

271   We analyzed 4,372 naturalized and 512 indoor populations. Our dataset included 323

272   species from 75 genera distributed over 479 regions (Figure 1). Globally, European and

273   North American regions had the highest number of indoor non-native populations, with the

274   highest number recorded in the UK, where 53 of the 61 non-native species with established

populations were restricted indoors (Figure 1a). Florida recorded the highest number of

naturalized non-native ant species (68 species naturalized; 0 species indoors) (Figure 1b).

There was a weak negative correlation between indoor and naturalized non-native ant

richness (Kendall's tau = -0.10).

Of the 323 non-native ant species analyzed, 29 species were considered harmful to the

environments or humans in a recent impact assessment (Gruber et al., 2022) (Table S4).

Twenty-one of these 29 harmful non-native species had populations confined to indoor

environments in at least one region, with a total of 300 indoor populations. European and

North American regions had the highest number of indoor harmful ant populations (Figure

1c), but not naturalized harmful ant populations (Figure 1d). Among the 137 regions with

≥1 indoor harmful ant population, Turkey exhibited the highest impact score in outdoor

environments (score=75; Figure 1e), while for socioeconomic impacts, the highest was

observed in Texas (score=53; Figure 1f).

The roles of climatic conditions in restricting non-native ants indoors

Using mixed effect logistic regressions, we found that ant species originating from

warm environments with a low temperature seasonality were more likely to be restricted

indoors when introduced to relatively colder environments with a higher temperature

seasonality (Figure 2, Table S5). However, regardless of climatic conditions in their

native ranges, non-native species had a high probability of establishing outdoors when

introduced to warm environments with a low temperature seasonality. The effects of

water availability, vertical habitat strata, and introduction year were minimal and thus

297   were dropped from the final model. Therefore, our final model only included the

298   interaction term between the temperature regimes in a species' introduced range and the

299   temperature regimes in its native range ($R^2_m = 0.52$; $R^2_c = 0.94$). We detected weak

300   phylogenetic (Moran's I = 0.01) and spatial autocorrelations (0.04) in the residuals of the

301   final model. Excluding potentially undersampled regions did not alter the conclusions

302   (Table S6).

303

304   **Predicted spread of indoor non-native ants under climate change**

305   Projecting the final model to future climate change scenarios, we found that the

306   average probability for 512 indoor non-native populations of 113 species to spread into

307   outdoor environments increased by 3.6% (range = 0–25.0%) and 14.2% (0–67.4%) under

308   the 2°C and 4°C warming scenario, respectively. We recorded similar increases for the

309   300 indoor populations of 21 harmful species analyzed, with the average probability

310   increased by 3.3% (0 – 24.7%) and 12.6% under the 2°C and 4°C (0–66.5%) warming

311   scenario, respectively.

312   Under the 2°C warming scenario, the average gain in naturalized non-native and

313   harmful species within regions through the spread of indoor populations was 2.0% (mean

314   species gain = 0.1; range = 0–1.5) and 3.3% (mean = 0.1; range = 0–0.6), respectively

315   (Figure 3a-d). Nevertheless, the increases relative to current naturalized non-native and

316   harmful species richness could be as high as 65.3% and 37.7% respectively, indicating

317   high variation among regions. The increases in non-native and harmful species richness

318   were higher under the 4°C warming scenario, with the former increasing by 8.1%

15

319 (average = 0.5; range = 0–5.2) and the latter increasing by 12.6% (average = 0.3; range =

320 0–2.0) on average. Again, we observed high spatial variation in the relative increases

321 across regions, with the number as high as 254.5% and 126.1% for non-native and

322 harmful species richness, respectively.

323

Potential impacts by indoor non-native ants under climate change

325 In both warming scenarios, we found that 69 of the 137 regions having ≥ 1 indoor

326 harmful population currently would have increased environmental impact scores in

327 outdoor environments, while 70 regions would have increased socioeconomic impact

328 scores. Enhanced competition (67 regions) would be the most prevalent environmental

329 impacts associated with the anticipated naturalization of harmful species populations

330 currently residing indoors, while crop loss (63 region) would be the most prevalent

331 socioeconomic impacts (Figure 4). The enhanced environmental and socioeconomic

332 impact scores would be strongly driven by the spread of indoor populations of

333 *Linepithema humile* in 28 regions (Figure S3).

334 Under 2°C and 4°C warming, the average increases in environmental impacts across

335 regions were 2.3% (mean score increase = 0.4; range= 0-4.1) and 9.2% (mean = 1.4;

336 range = 0-11.9), but maximum increases could reach 31.5% and 140.5%, respectively

337 (Figure 3e-f). Socioeconomic impacts within regions would also be increased by 2.2%

338 (mean = 0.2; range = 0-2.5) and 8.7% (mean = 0.9; range = 0-7.0) on average under 2°C

339 and 4°C warming, but maximum increases could reach 62.7% and 177.7%, respectively

340 (Figure 3g-h).

341   In all future climate scenarios, the projected gains in naturalized non-native and

342   harmful species, as well as the associated impacts, were largest in the Northern

343   Hemisphere, particularly in the USA and European regions such as Italy, France, and

344   Finland (Figure 4, Figure S4). Limiting warming to 2°C would reduce gain in naturalized

345   non-native and harmful ant species richness and the associated impacts, with the

346   reduction being more prominent in European regions and the USA (Figure S4).

347

348   **Countries' capacities to control the potential spread of indoor non-native ants**

349   We found that climate change effects on indoor non-native ant populations were

350   highly heterogeneous at the country level (Figure S5). In both warming scenarios, the top

351   10 countries were associated with > 65.0% of climate change effects, while the top 20

352   were associated with > 83.4% (Table S7). Most effects would be associated with

353   countries that had a total score ranging from 3-4 (Figure 5).

354   We detected the greatest shortfall in managing biological invasions (e.g., policies,

355   legislations, and resources targeting invasive species nationally), followed by monitoring

356   (e.g., facilities to report biological invasions) among the highly threatened countries

357   (Figure 6, Table S8). Depending on warming scenarios, only 25– 30% of the 20 most

358   threatened countries had "comprehensive" invasive species management, while 55 – 70%

359   had established monitoring schemes.

360

361   **Discussion**

17

362 We examined the effects of climatic conditions in restricting non-native ant populations

363 to indoor environments, and investigated whether climate change would facilitate the

364 spread of indoor non-native populations to outdoor environments (i.e., naturalization) and

365 potentially generate extra environmental and socioeconomic impacts. We further

366 evaluated whether these anticipated spreads would be concentrated in countries with high

367 abilities to respond and manage biological invasions (response capacity). We observed

368 that non-native ant species introduced to regions with low and seasonal temperatures had

369 a higher probability of establishing indoor populations if their native range had dissimilar

370 climates. However, climatic similarities between native and non-native regions largely

371 did not influence the naturalization success of non-native ant species in warm

372 environments with a low temperature seasonality. Our findings from a global analysis of

373 323 non-native ant species demonstrate the generalizing role of indoor environments as

374 unique microclimatic beachheads for non-native ants to bypass macroclimatic filters

375 posed by low and seasonal temperatures. This expands on previous studies focused on

376 individual regions and species (Hulme, 2015; Wang et al., 2015). Additionally, our

377 results suggest that the continuous warming of the global climate will erode

378 macroclimatic filters and facilitate the naturalization of non-native ant populations that

379 are currently confined to indoor settings, including species that cause negative impacts.

380 Warming extent is crucial in determining the increases in non-native species and

381 associated impacts, with all metrics increased by 2-3% and 8-9 under 2°C and 4°C

382 warming, respectively. Moreover, we found that the naturalization of indoor non-native

383 populations with climate warming is more likely to occur in regions lacking

384 comprehensive capacities to manage and monitor biological invasions. Altogether, these

385 findings highlight the role of indoor populations in exacerbating non-native ant invasions

386 globally under climate change, which is unlikely to be contained by current invasive

387 species management, adding to the already high negative impacts generated by invading

388 ants (Angulo et al., 2022; Gruber et al., 2022).

389   We found partial support for the climate matching hypothesis (Richardson & Pyšek,

390 2012), as increasing climatic similarities between native range and invaded regions were

391 important for outdoor establishments of non-native ants in cold environments with a high

392 temperature seasonality only. As with most macroecological studies, we cannot entirely

393 rule out the effects that geographic biases in sampling efforts worldwide have had on the

394 patterns observed (Hughes et al., 2021). Nevertheless, we re-analyzed our data by

395 excluding potentially undersampled regions and obtained similar results (S5). Thus, we

396 believe that our results reflect ecological processes rather than sampling biases, at least

397 for temperate regions, which are overrepresented in our analyses after excluding

398 undersampled regions. Our interpretation is further supported by physiological studies

399 showing that the average critical minimum thermal limit of ant species lies at 5°C

400 (Nascimento, Câmara & Arnan, 2022), which is often exceeded in the winter of

401 temperate environments (Abatzoglou et al., 2018). In contrast with cold regions, all non-

402 native ant species had a high probability of establishing in warm regions. One

403 explanation is that air and soil temperatures at regional levels rarely exceed the average

404 critical maximum thermal limit for ants, which lies at 46°C (Abatzoglou et al., 2018;

405 Nascimento et al., 2022). Nevertheless, heat stress in warm regions can still cause

406 substantial lethal and sublethal effects on ants, such as increasing predation risks or

407 reducing colony size (Leong, Hui & Guénard, 2023; Penick, Diamond, Sanders & Dunn,

19

408 2017). Unlike lethal effects, sublethal effects might not act to restrict non-native ant

409 species to indoor environments, but only increase their associations with such

410 environments.

411   As climatic conditions in indoor and outdoor environments can be largely

412 decoupled, indoor records should be excluded from distributional data if studies are

413 primarily interested in assessing the risks of outdoor environments to biological invasions

414 or how species expand their niche through invasions. Popular sources of distributional

415 data, such as GBIF, can contain indoor records, and previous studies do not always

416 remove these observations before analyses (Arnan et al., 2021; Jung, Kim, Jung & Lee,

417 2022; Lee, Jung, Lee, Lee & Jung, 2021; Zhao et al., 2023). When indoor records are

418 very prevalent in a dataset, or when they act as outliers (Liu, White & Newell, 2018;

419 Rödder & Engler, 2011), climatic niche and species' abilities to establish under novel

420 climate can be overestimated, subsequently leading to erroneous risk assessments (Roy et

421 al., 2018) on sites susceptible to invasions and species likely to become invasive.

422 Including indoor records can also influence conclusions of processes driving invasion

423 patterns, such as reducing the importance of climate matching due to the lack of

424 macroclimatic filters in indoor environments, and increasing the importance of propagule

425 pressure (Lockwood et al., 2005), potentially misleading management practices.

426   Our findings reveal a lack of comprehensive capacities to control or prevent future

427 biological invasions among countries that are highly susceptible to the spread of indoor

428 non-native populations to outdoor environments. These shortfalls are mainly related to

429 the management and monitoring of biological invasions, indicative of a lack of

430   awareness, resources, personnel, and information (Early et al., 2016). Such countries

431   could have limited implementations of measures controlling or eradicating indoor non-

432   native populations, especially as these measures are often voluntary (Hulme, 2015).

433   Additionally, a country's limited response capacity can exacerbate the difficulties it faces

434   in incorporating the effects of climate change into invasive species management due to

435   overwhelming demands from current invasions (Beaury et al., 2020). The lack of

436   planning for climate change can impede early detection and rapid response in indoor and

437   outdoor environments in the future, which are crucial to minimizing the negative impacts

438   of biological invasions (Reaser et al., 2020).

439   In this study, we aimed to examine the importance of climatic drivers in restricting

440   non-native ant species to indoor environments, at least for species that are likely to escape

441   (i.e., excluding species that are pets and restricted within terrariums (Wang et al., 2023)).

442   We did not seek to undertake a comprehensive assessment of the effects of climatic

443   drivers on biological invasions, as this would require information on failed establishment

444   events following introductions, for which data are presently unavailable. Thus, our

445   climate change projections solely relate to the effects of climate change in facilitating the

446   spread of indoor populations to outdoor environments, and should not be interpreted as

447   absolute forecasts of future non-native species richness in the outdoor environments of

448   different regions. Still, our results evidence how warming can systematically exacerbate

449   the impacts of a key but poorly understood invasion pathway—populations of non-native

450   species residing indoors (Hulme, 2017).

21

451   Overall, our results provide evidence that indoor environments are important

452 microclimatic beachheads for the invasions of non-native ants to regions with low and

453 seasonal temperatures, especially for species that originate from regions with dissimilar

454 temperature regimes. The continuation of climate warming is expected to facilitate the

455 naturalization of indoor-confined non-native ant species and cause extra socioeconomic

456 and environmental impacts, with the average increases across regions tripled under the

457 4°C warming compared with the 2°C warming scenario. Although our analyses are

458 restricted to ants, these findings should apply to taxa that display high non-native species

459 richness indoors, such as various terrestrial invertebrates (Kenis et al., 2007; Kobelt &

460 Nentwig, 2008; Roques et al., 2009), plants (van Kleunen et al., 2018), and fungi

461 (Bradshaw et al., 2022). These three taxa are known to contain some of the worst

462 invaders, therefore the naturalization of their indoor populations should also lead to extra

463 environmental and socioeconomic impacts under climate change (Diagne et al., 2021;

464 Luque et al., 2014). Managing the extent of warming could be key in limiting impacts

465 contributed by the spread of indoor non-native populations to outdoor environments.

466 Failure to limit warming would require strengthening response capacities, especially in

467 the management and monitoring of non-native species, to minimize the impacts of these

468 anticipated invasions.

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470 **Conflict of Interest Statement**

471 The authors declare no conflict of interest.

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473   **Data Availability Statement**

474   The data and R scripts supporting the findings of this study are available in an

475   anonymized repository https://anonymous.4open.science/r/Indoor_ants-

476   C440/README.md. The finalized version will be uploaded to Github and Zenodo after

477   acceptance.

478

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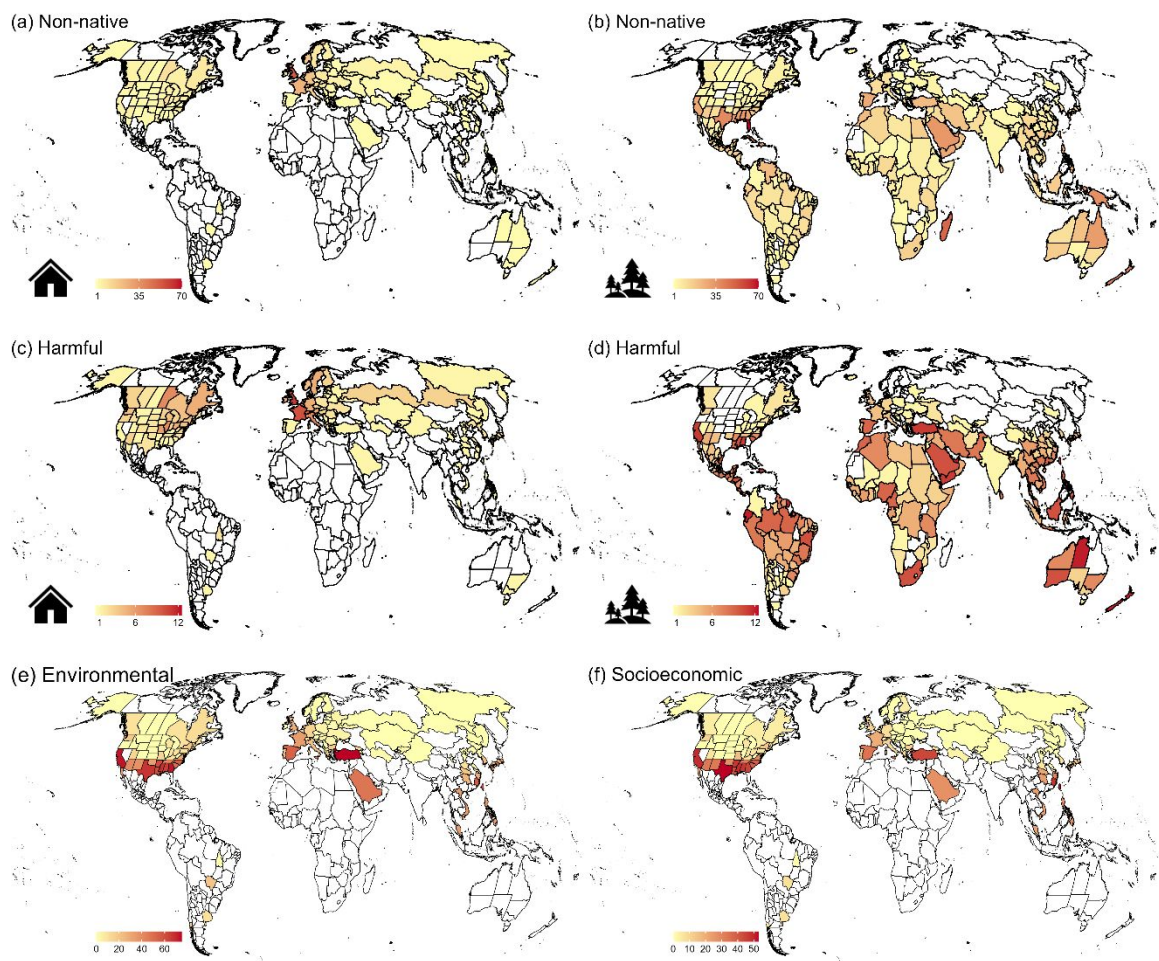
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Figure 1. Global distribution of non-native (a,b) and harmful (c,d) ant species richness in indoor (a,c) and outdoor (b,d) environments used in the analyses, as well as cumulative environmental (e) and socioeconomic impact scores (f) in outdoor environments. Populations without dated records and species without native distribution data were excluded, although this only represents ~5% of the data. In panel a-d, regions in white lack records for non-native (a,b) and harmful (c,d) ant species established in indoor and outdoor environments. In panel e-f, regions in white lack harmful species restricted indoors. Higher values in panel e and f indicate higher impacts of harmful ants in outdoor environments.

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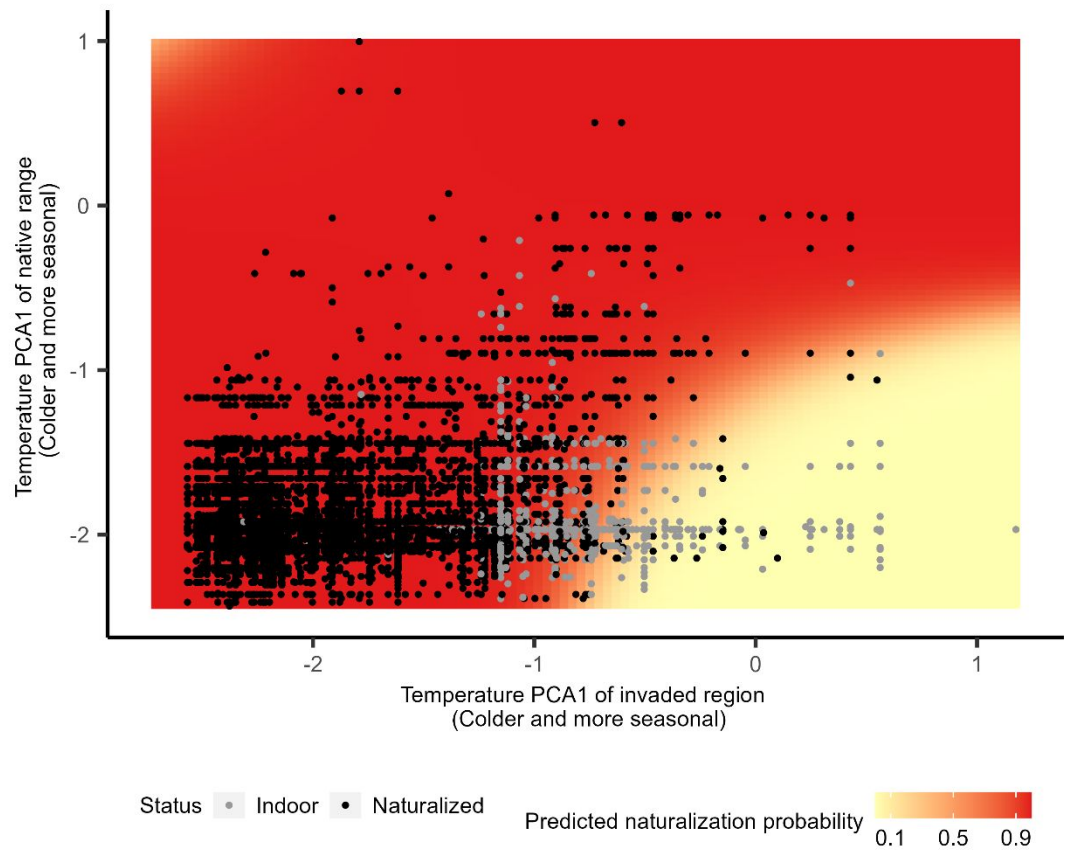48
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Figure 2. Differences between naturalized (black dots) and indoor ant species (grey dots)

in relation to temperature and seasonality of the native and invaded ranges. Species

originating from cold environments have a higher probability of establishing outdoors

(top right corner) compared with species originating from warm environments when

invading cold regions (bottom right corner). In warm regions, however, all incoming non-

native species are expected to establish outdoors regardless of the climate of their native

range (left side). Extremely cold-distributed species could have a lower probability of

outdoor establishment in very warm regions (i.e., upper left corner), although these apply

to hypothetical scenarios only (top left corner). Each data point represents a non-native

species established in an introduced region, with grey and black colours representing

657   establishments in indoor and outdoor environments, respectively. Increasing PCA1 scores

658   along both axes indicate colder and more seasonal temperature regimes, with Y-axis and

659   X-axis indicating the climate in the native range of each species, and the climate in the

660   invaded region of each population, respectively. Predicted naturalization probabilities are

661   based on the fixed (but not random) effects of the full model.
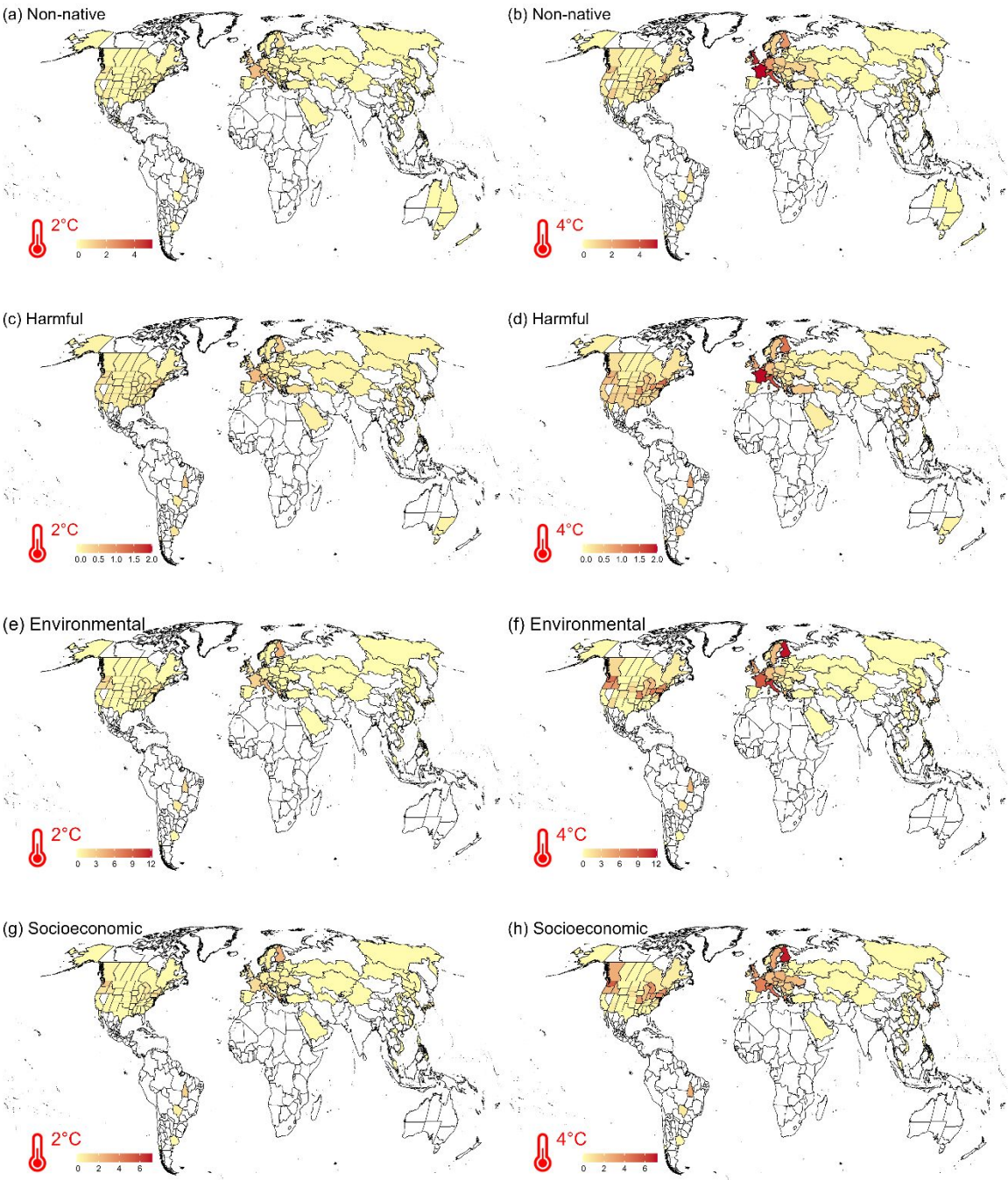
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Figure 3. Projected gains in non-native species (a,b), harmful species (c,d),

environmental impacts (e,f), and socioeconomic impacts (g, h) in outdoor environments

under 2°C and 4°C warming. Regions in white lacks indoor non-native (a,b) and harmful

668   populations (c-h). Projections are based on the random and fixed effects of the final
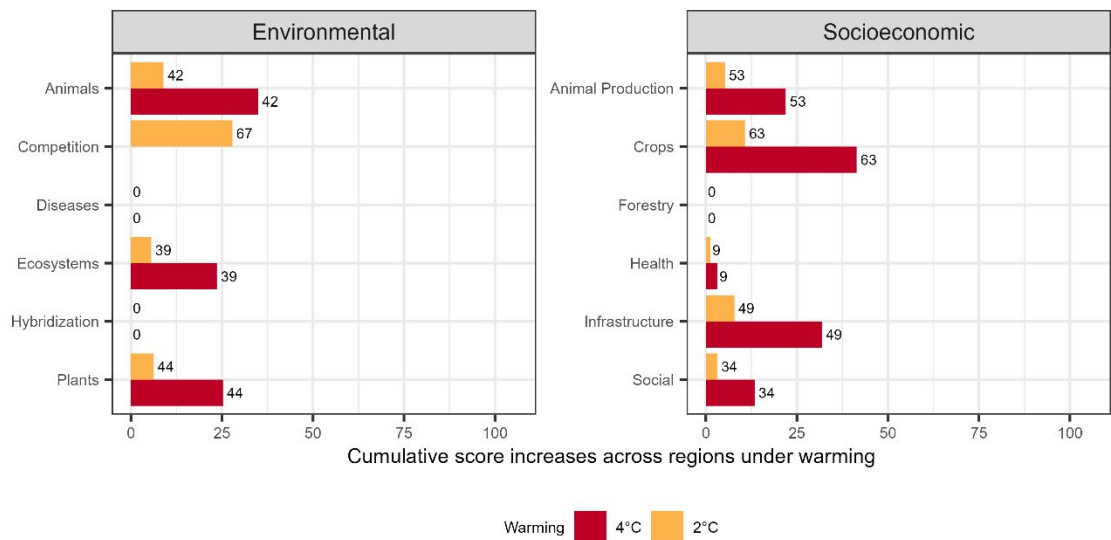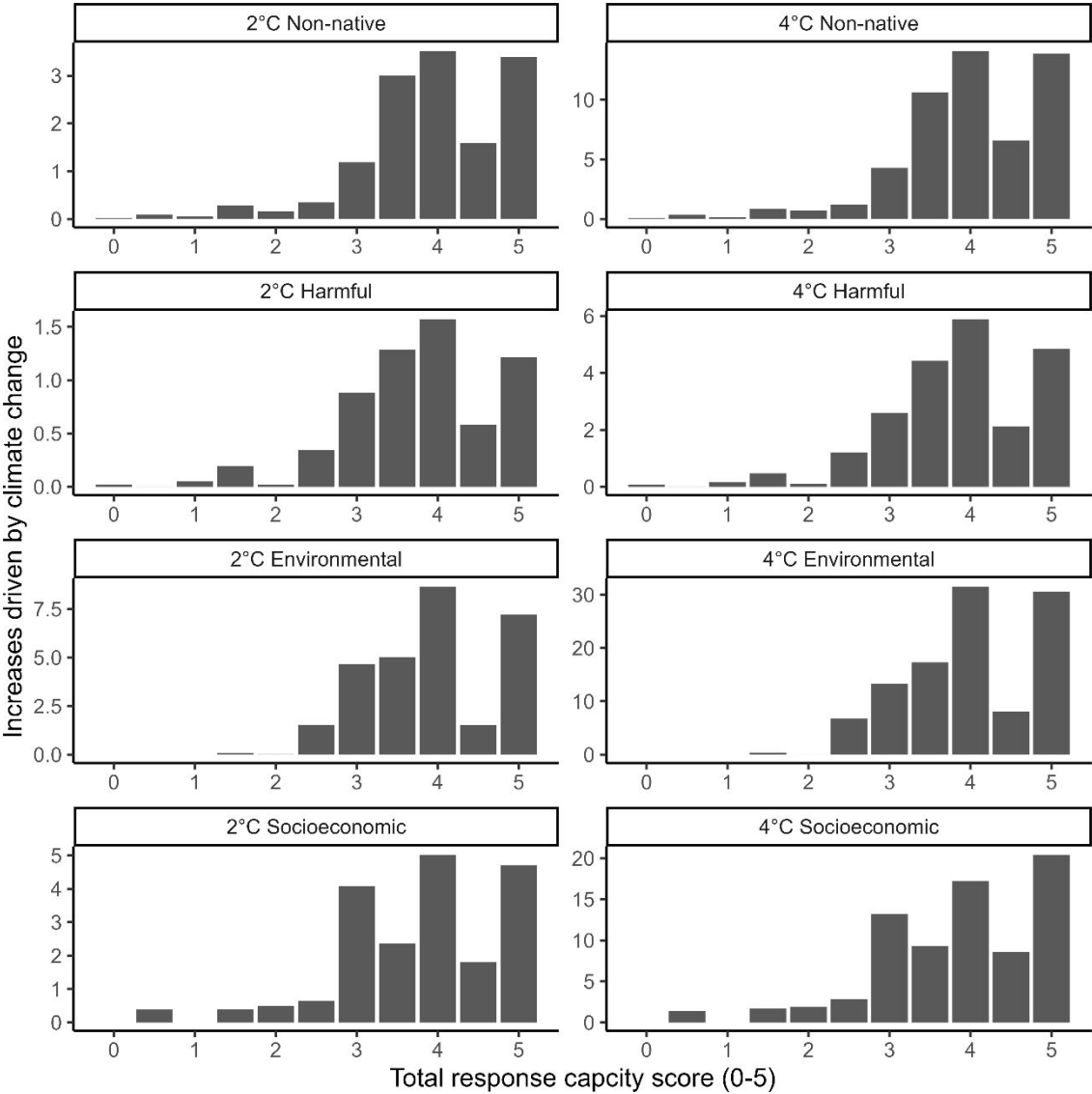
669   model.

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Figure 4. Cumulative score increases across regions for different impact categories under two warming scenarios. A higher increase in impact scores indicates the negative effects become stronger under warming. The number beside each bar represents the number of regions with increased impacts.

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678   **Figure 5.** The impacts of climate change in facilitating the spread of indoor non-native

679   population to outdoor environments across different levels of total response capacity.

680   Climate change impacts are calculated as the sum of gain in naturalization probability,

681   environmental impacts, and socioeconomic impacts across countries with the same total

682   response capacity scores. Thus, a higher value along Y-axis indicates more severe

683   impacts of climate change. A higher score in response capacity (i.e., X-axis) indicates

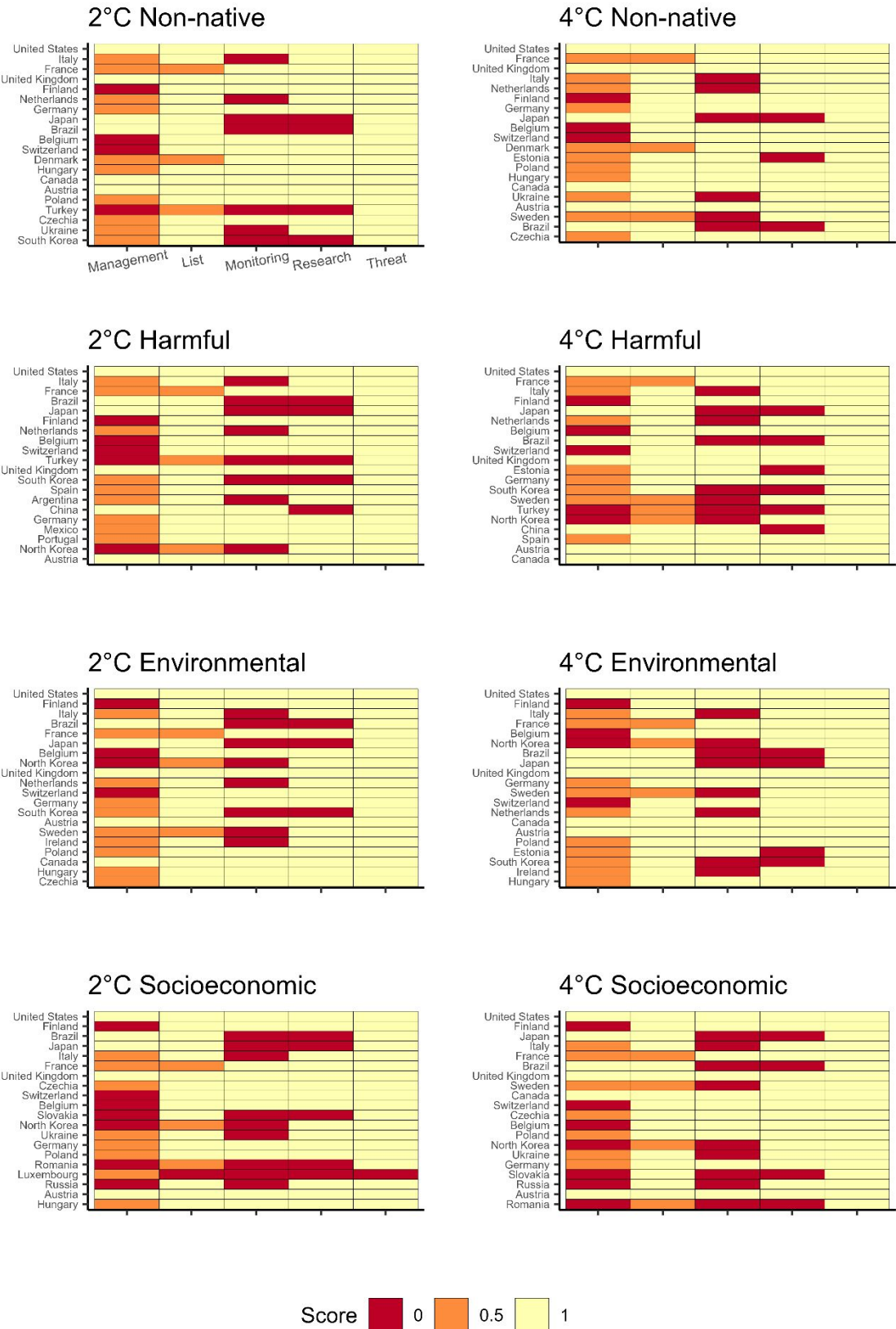684   more comprehensive policies on biological invasions.

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Figure 6. Scores of response capacity in top-20 countries with the highest projected gains

689   in non-native or harmful species in outdoor environments under two warming scenarios.

690   Countries at the top of the y-axes are projected to experience the highest gains in the

691   species richness of non-native or harmful ants due to the anticipated spread of indoor

692   populations to outdoor environments under climate warming. A country with

693   comprehensive policy in certain aspects would be scored as 1.

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1   **Supporting Information Text S1 – Detailed descriptions of each database**

2   **Non-native ant records**

3   The Global Ant Biodiversity Informatics (GABI) extracted nearly two million ant

4   occurrence records from the literature (10,700 publications) and specimen databases,

5   such as AntWeb, museum collections, and personal collections. GABI records were

6   compiled and checked by ant experts to maximize reliability (Guénard, Weiser, Gomez,

7   Narula & Economo, 2017). To maximize the geographic resolution of the distribution

8   data and as many records (especially older records) were not georeferenced, a system of

9   546 polygons was used for analyses, where an occurrence record could correspond to

10   either a country or a lower administrative unit for large countries such as China and the

11   United States. Some records reflected natural rather than political boundaries, such as

12   island systems, including the Lesser Antilles (see details in Guénard et al. (2017)). The

13   database used species' mentions in the literature, their number of records within a

14   zoogeographical realm or region, and the locality and habitat of the collection to

15   determine the native and non-native range of each species. Subspecies were considered

16   separately in the database, but hereby we collectively term them as species.

17   We defined the indoor status of each non-native record following terminologies

18   from the database (Wong, Economo & Guénard, 2023). "Indoor" was defined as

19   populations only occurring in indoor environments such as greenhouses and buildings,

20   while "Naturalized" was defined as populations established in outdoor environments.

21   Any records of non-native ants merely intercepted at borders or which reflected an

22   uncertain introduction and indoor status were excluded from the analysis. Where there

23   were multiple occurrence records for the same non-native species within a region, we

24   classified that population (i.e., unique combinations of regions and species) as "indoor"

25   only if all records unanimously suggested that the species was restricted to indoor

26   environments in the region, and classified the species as "naturalized" if the different

27   records had conflicting statuses.

28   The year of each record was either their publication year, or the time that the record

29   was made according to the literature. This information would be used as a proxy for the

30   year of introduction in each region. For example, as *Linepithema humile* had eight dated

31   records in the UK between 1915–2016, with seven as "indoor" and one as "naturalized",

32   we considered this species to be "naturalized" in the UK and introduced in 1915.

33   Note that our dataset did not address non-native ants from pet trade, which would

34   also be considered as indoor records by definitions. However, these pets were often

35   contained within terrariums, thus they are unlikely to escape and establish outdoors, even

36   if outdoor conditions are suitable for them. This would make them unsuitable for testing

37   our hypotheses on the role of climatic conditions in restricting non-native ant indoors.

38

39   **Environmental and socioeconomic impacts of non-native ants**

40   Previous studies have assigned impact scores for each non-native species and obtained

41   the sum of these scores for each region to assess the potential impacts of biological

42   invasions and prioritize regions for management (Bai, Chisholm, Sang & Dong, 2013;

43   Katsanevakis, Tempera & Teixeira, 2016). We obtained the scores of environmental and

44   socioeconomic impacts by non-native ants from Gruber et al. (2022) to understand the

45   potential consequences of indoor non-native ant populations spreading into outdoor

46   environments. We used the scores of each non-native ant species in the Generic Impact

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47   Score System (GISS), a methodology considering the environmental and socioeconomic

48   impacts of non-native species. We chose to use GISS instead of other methodologies

49   because they provided finer classifications of different impacts, and the scores were based

50   on 1,162 impact records from 642 studies. Environmental impacts contained six

51   categories: 1) plants or vegetation, such as non-native ants affecting other ant species and

52   ultimately seed dispersal; 2) animals through predation, parasitism or intoxication; 3)

53   competition with other species; 4) ecosystem impacts, such as driving invasion

54   meltdown; 5) disease transmission; 6) hybridization. Socioeconomic impacts also

55   contained six categories: 1) Crop production; 2) Animal production; 3) Forestry

56   production; 4) Human infrastructure and administration, such as electrical damage and

57   costs of managing invaded areas; 5) Human health 6) Social life, such as abandoning

58   playgrounds due to ant infestation. The score of each category ranged from zero (i.e., no

59   impact) to five (i.e., severe impacts), thus theoretically a species can have 60 points in

60   total, although the highest score was 35 only when considering the maximum scores of

61   each category (Gruber et al., 2022).

62   We excluded all low-confidence impact records. For human health impacts, we

63   further removed records that are unlikely to occur within outdoor environments, as our

64   studies are interested in the potential consequences of naturalization under climate

65   change. Specifically, for health impacts, we only considered records of ant attacks, even

66   if these attack records were conducted in indoor environments, as ants could attack

67   people outdoors. We excluded scores based on ants carrying pathogens, which is a health

68   concern in indoor environments such as food storage facilities due to the potential of food

69   poisoning, but is a lesser concern in outdoor environments. Additionally, ants are likely

70   to acquire these pathogens when they forage in contaminated areas such as hospitals, thus

71   naturalized populations do not necessarily carry the same pathogens (Alharbi, Alawadhi

72   & Leather, 2019). Scores based on ant occurrences within indoor environments only were

73   not considered, because these studies did not provide any evidence of their direct or

74   indirect health impacts, even though ant species were perceived as "nuisance" or

75   "hygiene issues" within indoor environments. Thus, seven "harmful" species had no

76   negative impacts in outdoor environments (e.g., *Monomorium pharaonis*).

77

78   **Current and future climatic conditions of each region**

79   As the dataset included a variety of soil-dwelling, surface-dwelling and arboreal ant

80   species (Wong et al., 2023), we characterized the climatic conditions of each polygon

81   using the monthly minimum and maximum air temperature, total precipitation, and soil

82   moisture from the open-access database TerraClimate, which has a ~4 km spatial

83   resolution for current and future climate scenarios (Abatzoglou, Dobrowski, Parks &

84   Hegewisch, 2018). We characterized each grid using the minimum temperature of the

85   coldest month, maximum temperature of the warmest month, total precipitation and soil

86   moisture in both the driest and wettest month. Additionally, we calculated the standard

87   deviation across months for temperature, soil moisture and precipitation separately as a

88   measure of seasonality. For temperature, we calculated the average across the minimum

89   and maximum temperatures in each month, and obtained the standard deviation across all

90   months as a measure of temperature seasonality. We also extracted the minimum and

91   maximum soil temperatures of the coldest and warmest months at 0-5 cm and 5-15 cm

92   deep from SoilTemp (8), but these data were not included in subsequent analyses because

4

93   forecasts for the impacts of climate change on soil temperatures were unavailable.

94   However, the omission of soil temperature is unlikely to affect our results since they were

95   highly correlated with air temperature under current climatic conditions (Pearson's r >

96   0.91). We included the 2°C and 4°C warming scenarios, with the former representing the

97   upper limit of global warming target indicated in the Paris Agreement, and the latter

98   representing a "business-as-usual" outcome.

99   We first conducted a collinearity check on each climatic variable across the globe

100   and found high intercorrelations (R > 0.7 or < -0.7). Therefore, we conducted PCAs

101   separately for temperature and water variables based on current climatic conditions after

102   standardization and extracted PCA1 scores for both, as they explained 76% and 62% of

103   variations, respectively. We did not retain other PCA axes as their explanatory power was

104   not higher than random, based on a significance test in R-package *BiodiversityR* (Kindt,

105   2023). Increasing PCA1 scores for all temperature variables indicated cooler and more

106   seasonal environments, while for water variables, they indicated wetter and more

107   seasonal environments. We then reprojected the two PCA models using future climatic

108   conditions to obtain future PCA1 scores of each grid.

109

110   **Response capacity**

111   To quantify response capacity to biological invasions, we used the database from (9),

112   which scored countries' abilities to address invasive species threats in 2015 based on

113   countries' reports to the Convention of Biological Diversity

114   (https://www.cbd.int/reports). Dependent territories (e.g., overseas territories of France

115   and UK, US minor outlying islands) were considered as separate units, and no scores

116   were available for these regions.

117   The response capacity scores have been used to assess general response capacities to

118   a variety of invasive taxa (e.g., (Faulkner, Robertson & Wilson, 2020)). Here, the scores

119   were used as a proxy of response capacity to ant invasions, even though the scores were

120   based on all taxa and not specific to ants. The database provided scores on six aspects of

121   invasive species management, including whether 1) invasive species were recognized as

122   threats to the economy and biodiversity of the country, 2) a national list of current and

123   potentially problematic invasive species had been made, 3) there were management

124   practices to regulate impacts of invasive species 4) there were measures to manage

125   potential introductions of invasive species 5) there were international collaborations or

126   research on controlling invasive species and 6) invasive species were monitored for

127   potential expansion and emergence, including monitoring programs and awareness-

128   raising campaigns. Since we were interested in the effects of non-native ant populations

129   which had already been established, we did not consider if there were measures to

130   manage introduction (factor 4). Generally, these factors were either scored using two

131   ("No" [0] / "Yes" [1]) or three categories ("None" [0] / "Limited" [0.5] /

132   "Comprehensive" [1]). Note that the scores were comparative, and even countries with

133   the highest scores could have insufficient capacity to manage biological invasions (Early

134   et al., 2016). Nevertheless, the scores still captured capacity differences across countries

135   and could be used to assess if any effects of climate change on the spread of indoor non-

136   native ant populations to outdoor environments would be limited to relatively well-

6

137   managed countries. Additionally, the scores would help identify the weakest aspects of

138   invasive species management in highly threatened countries.

139

140   **References for Text S1**

141   Abatzoglou, J. T., Dobrowski, S. Z., Parks, S. A., & Hegewisch, K. C. (2018).

142   TerraClimate, a high-resolution global dataset of monthly climate and climatic water

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158   ants reveals new insights for risk assessment. *Ecological Applications*, *32*(4), e2577.

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160   Global Ant Biodiversity Informatics (GABI) database: synthesizing data on the

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162   *News*, *24*, 83–89.

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169   capacities of non-native ants. *Current Biology*, *33*, 566–571.

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171

172   **Supporting Information Text S2 – Upscaling regional impacts to the country levels**

173   We used the maximum projected gain in outdoor establishment probability,

174   environmental impacts, and socioeconomic impacts under climate change to represent

175   each species with ≥ 1 indoor population within a country. For example, *Monomorium*

176   *floricola* had three indoor populations in the US, and we used the population in the

177   District of Columbia for country-level analyses, as it had the highest projected gain under

178   climate change. We then summed the gain in outdoor establishment probability,

179   environmental impacts, and socioeconomic impacts across species within each country to

180   represent climate change effects. These metrics reflect how climate change will drive

181   indoor populations to spread into outdoor environments, expanding their distribution

182   within countries and increasing impacts. Note that gains in outdoor establishment

183   probability does not reflect gains in non-native or invasive species richness at the country

184   level because some indoor populations have naturalized in other regions within the same

185   country.

186   In some regions where one country has a disproportionately larger area than others,

187   we used the largest country to represent the region. Examples include the region

188   "continental Italy" represented by Italy despite the presence of Vatican and San Mariano,

189   and "Malaysia and Singapore" represented by Malaysia. There were regions associated

190   with multiple countries with more comparable size (e.g. "Borneo", "Israel and Palestine",

191   "Sudan", "Cyprus"), but they did not contain any indoor populations and therefore would

192   not affect the country-level analyses.

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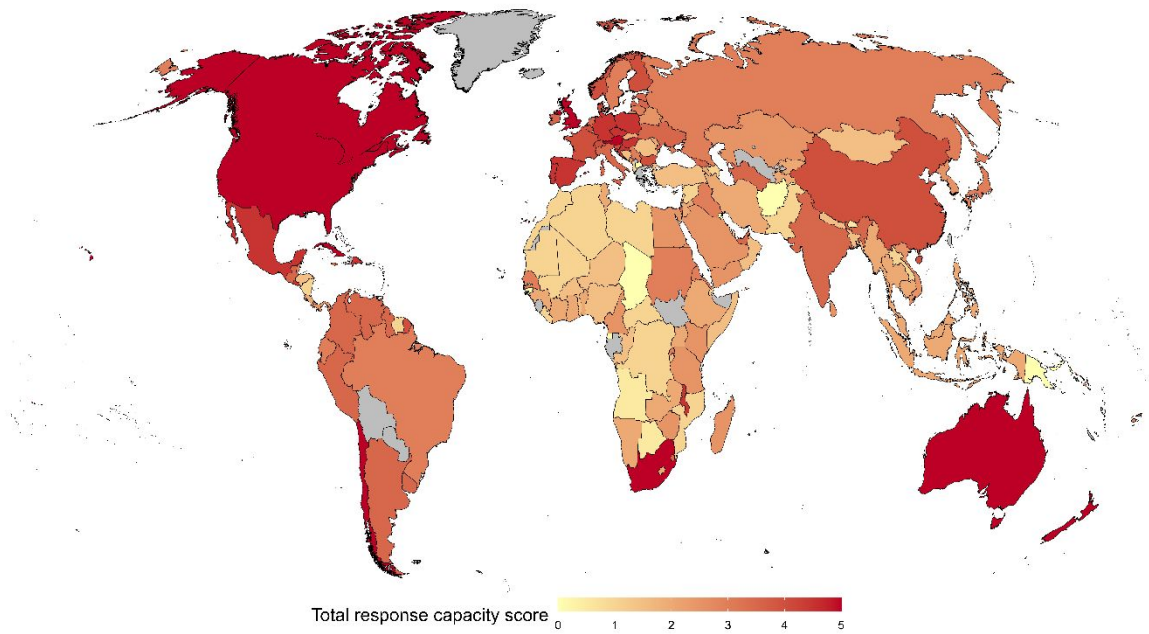16
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195 **Figure S1.** Total response capacity score across different countries following Early et al.

196 (2016). Higher scores indicate better response capacity.
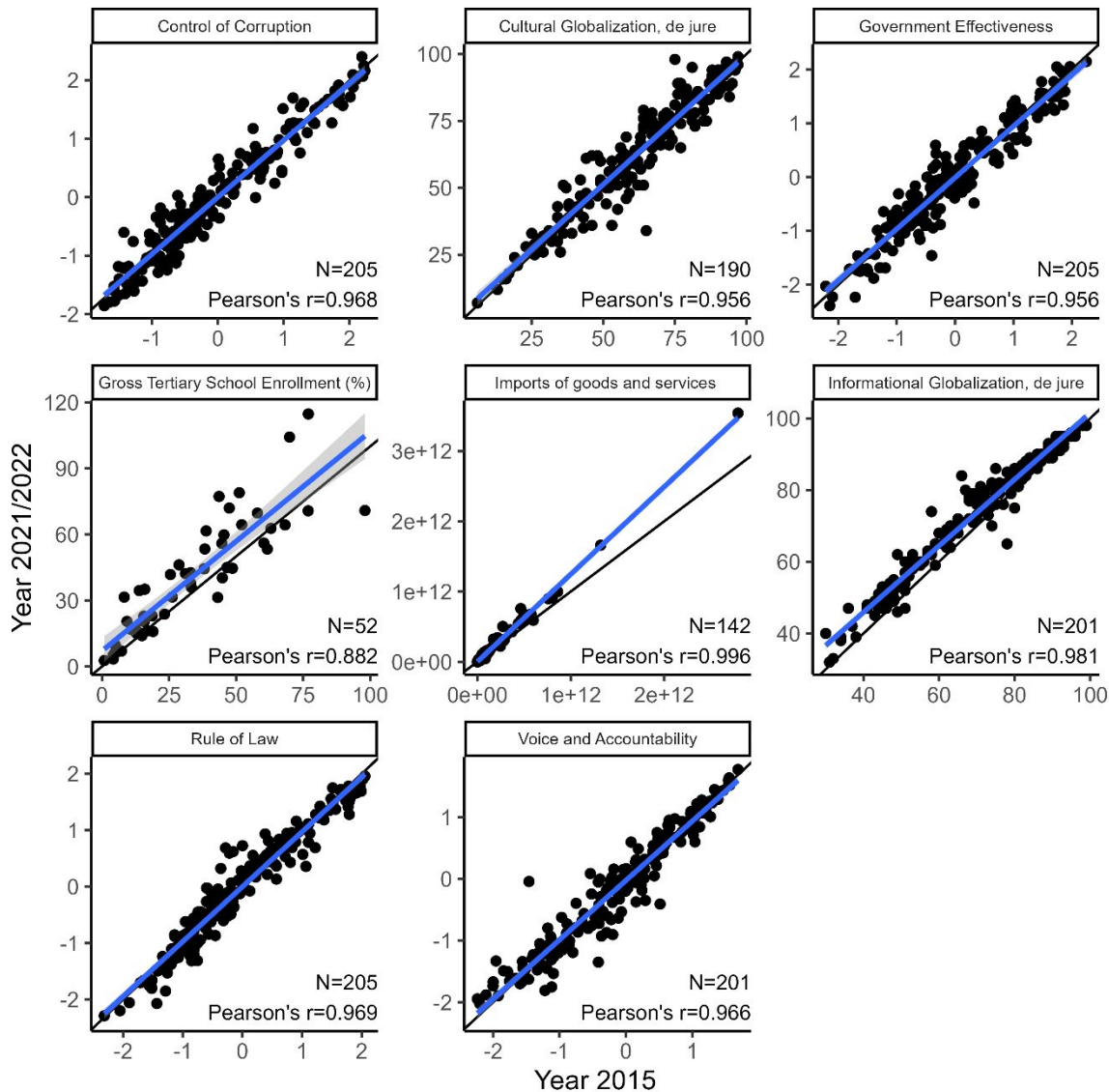
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Figure S2. Correlations between socioeconomic conditions in 2021/2022 and 2015. Blue lines represent fitted relationships, while the black lines represent no changes in the socioeconomic conditions across the two time periods. Shaded areas are 95% confidence intervals of the fitted relationships. See Table S1 for additional explanations of each variable.
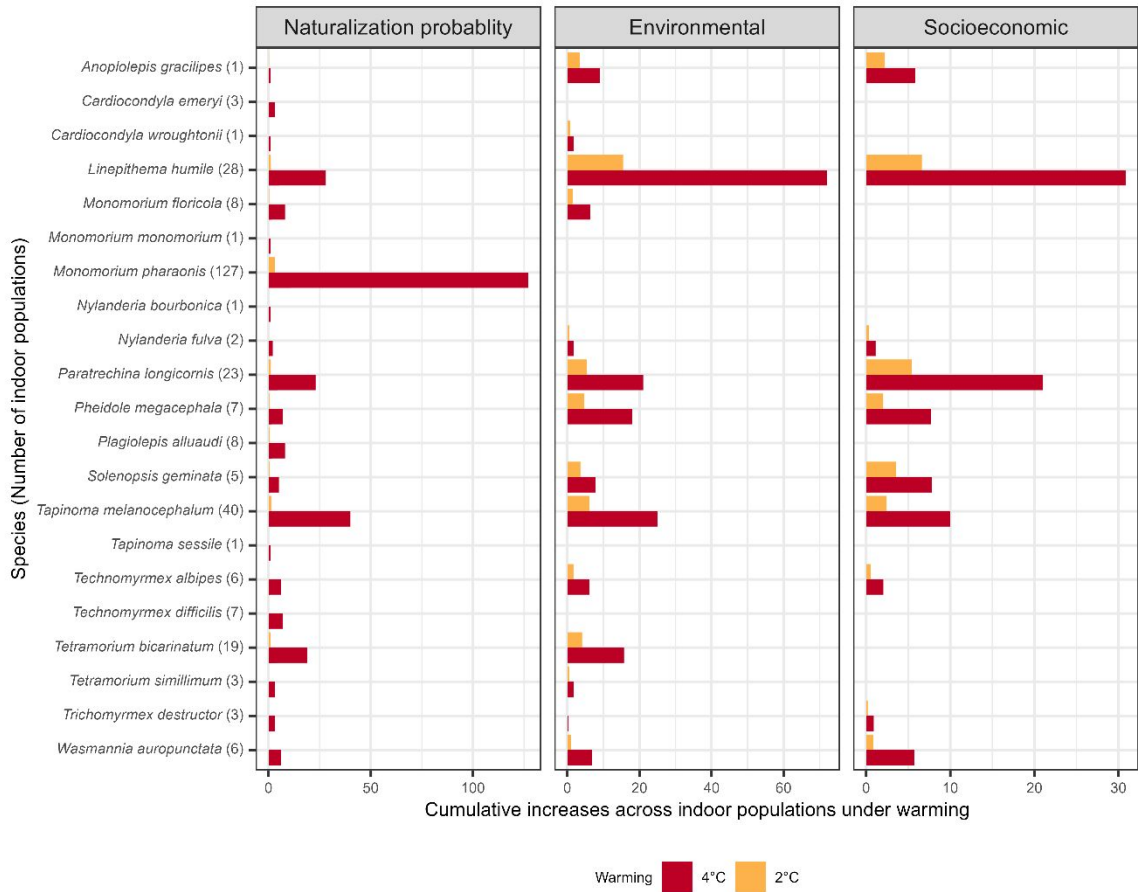
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Figure S3. The cumulative increase in naturalization probability, environmental impacts, and socioeconomic impacts associated with each harmful species across all indoor populations under two warming scenarios. A larger increase indicates climate change facilitates the naturalization of the species and their associated impacts more strongly. Some well-known non-native ants with negative impacts such as *Solenopsis invicta*, *Brachyponera chinensis* are not shown here due to a lack of indoor record at present.
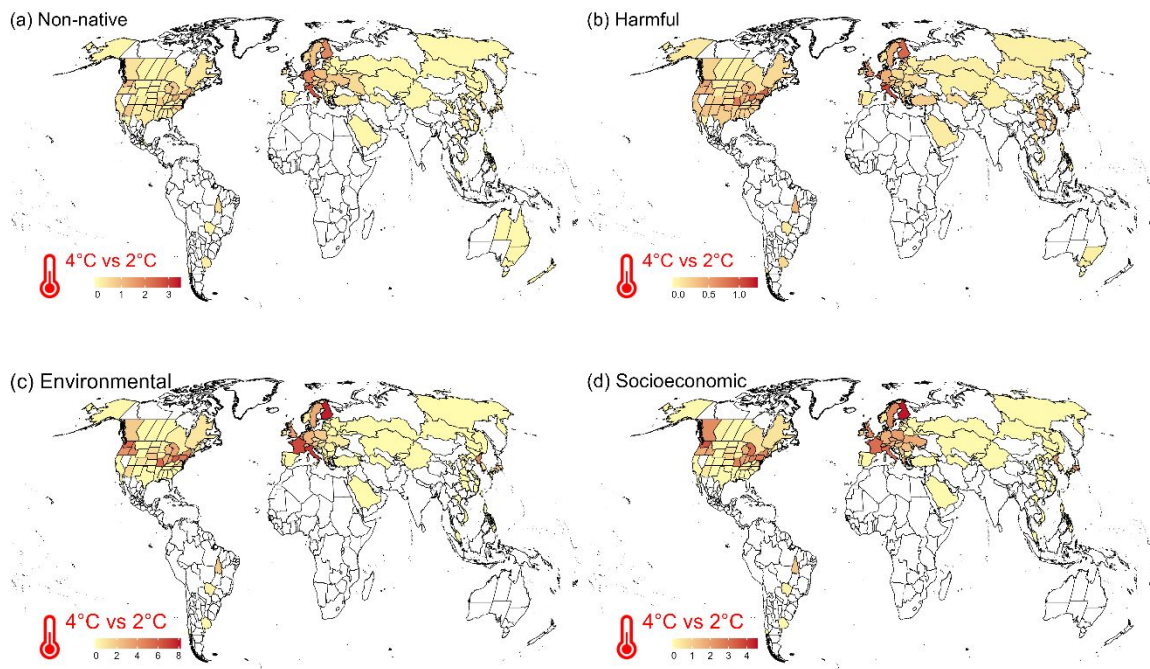
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Figure S4. Additional gains in non-native (a) and harmful species richness (b), environmental impacts (c), and socioeconomic impacts (d) under 4°C warming compared to 2°C warming.
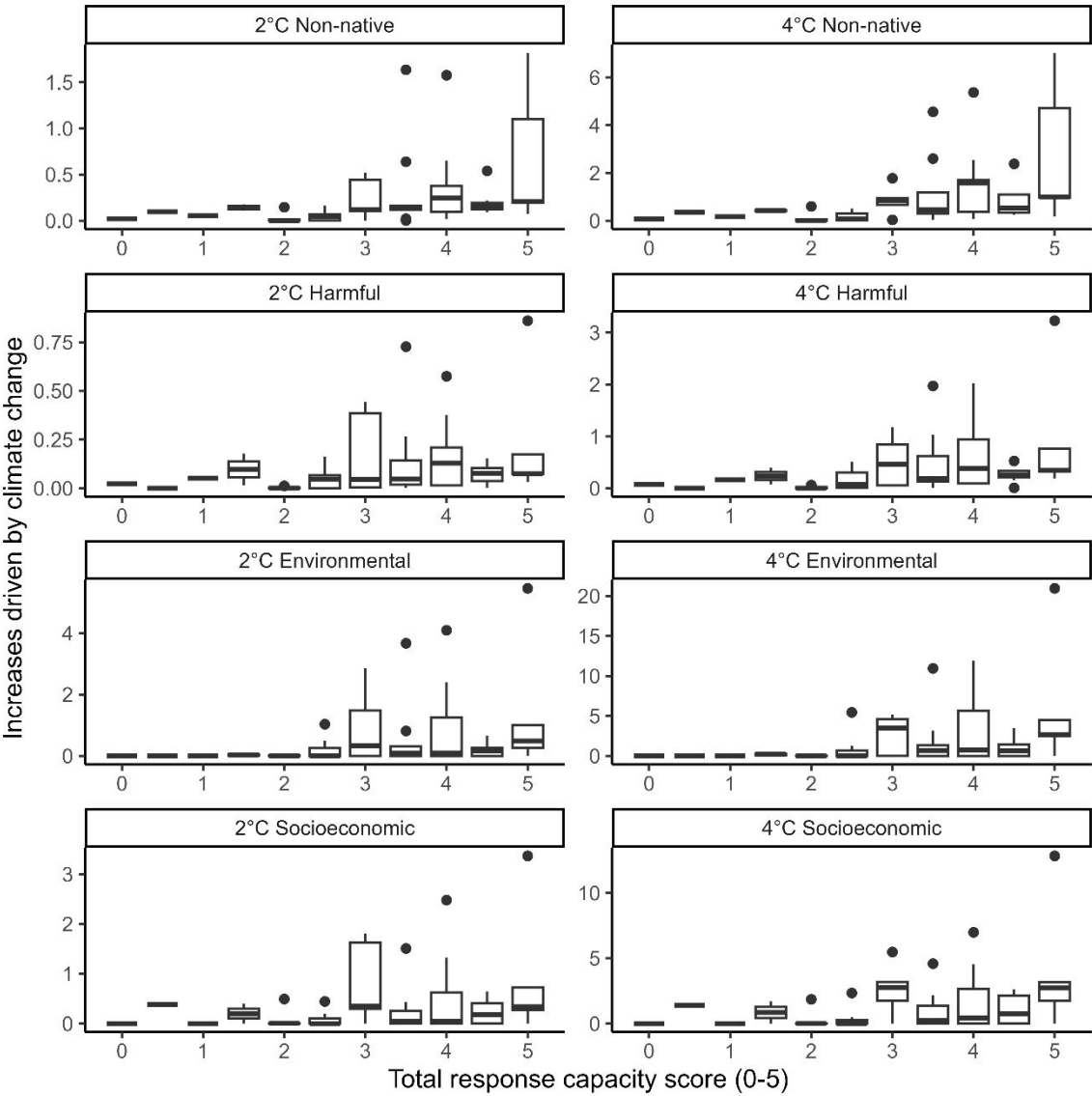
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Figure S5. Climate change impacts across countries with different levels of response

capacity (n = 54). Climate change impacts are calculated as the sum of gain in

naturalization probability.

222 Table S1. Details of socioeconomic variables important in determining response

223 capacities of countries, as demonstrated in Latombe et al. (2023). Note that in contrast

224 with Latombe et al. (2023), we used gross tertiary school enrollment instead of average

225 education levels because the former has more updated data. Correlations were conducted

226 between 2015 and the most updated information on each socioeconomic variable (2021

227 or 2022). All data were at country levels.

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Names	Description	Source
Control of corruption (2015,2022)	Scores are based on perceptions and range between -2.5 and 2.5, with higher scores indicating better control.	The World Bank, 2024
Government effectiveness (2015,2022)	Scores are based on perceptions and range between -2.5 and 2.5, with higher scores indicating higher effectiveness.	The World Bank, 2024
Gross tertiary school enrollment (2015,2022)	Number of students enrolled in tertiary education regardless of age relative to the number of students belonging to the official age group corresponding to tertiary education. Values are multiplied by 100 and thus in percentage. Higher values indicate higher capacities of countries' education systems.	The World Bank, 2024
Imports of goods and services (2015,2022)	Total values of all goods and services from other countries. The values reflect prices in 2015 in USD. Higher values indicate more imports.	The World Bank, 2024
Rule of law (2015,2022)	Scores are based on perceptions and range between -2.5 and 2.5, with higher scores indicating higher confidence in the rules of society.	The World Bank, 2024
Voice and Accountability (2015,2022)	Scores are based on perceptions and range between -2.5 and 2.5, with higher scores indicating better accountability.	The World Bank, 2024
Cultural Globalization, de jure (2015,2021)	The index reflects the combinations of gender parity, human capital, and civil liberties. A higher value indicates that countries are more globalized in the three cultural aspects.	Dreher, 2006; Gygli, Haelg, Potrafke & Sturm., 2019

15

Informational Globalization, de jure (2015,2021)	The index reflects the combinations of television access, press freedom, and internet access. A higher value indicates that countries are more globalized in the three aspects.	Dreher, 2006; Gygli et al., 2019

229

230   References for Table S1

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238   to reduce biological invasions. *Sustainability Science*, *18*(2), 771–789.

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240   https://databank.worldbank.org/source/world-development-indicators. Accessed on

241   2024-03-03.

242

243   Table S2. PCA results based on temperature and water availability variables. Only the

244   results of the first two axes are shown as they have the highest explained variance. All

245   variables were standardized before the analyses.

PCA on temperature variables		
	PC1	PC2
Minimum temperature of the coldest month	-0.65	-0.08
Maximum temperature of the warmest month	-0.57	-0.61
Standard deviation of monthly temperature (Seasonality)	0.50	-0.79
Explained variance	77.8%	21.9%
Significant	Yes	No

PCA on water availability variables		
	PC1	PC2
Total precipitation in the driest month	0.17	0.84
Total precipitation in the wettest month	0.46	0.32
Standard deviation of monthly total precipitation (Seasonality)	0.47	0.07
Soil moisture in the driest month	0.32	-0.26
Soil moisture in the wettest month	0.48	-0.28
Standard deviation of monthly soil moisture (Seasonality)	0.46	-0.22
Explained variance	62.7%	18.1%
Significant	Yes	No

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248   Table S3. Missing genera from the phylogenetic tree and their placement. If possible, we

249   placed each missing genus according to molecular phylogeny data. If not, they were

250   assigned to the closest genus based on previous placement before they were upgraded to

251   genus level. For example, *Erromyrma* was previously placed in *Monomorium*.

Missing genus	Sister1	Sister2	References
Chelaner	*Austromorium*		(Sparks, Andersen & Austin, 2019)
Colobopsis	*Calomyrmex*	*Opisthopsis*	(Ward, Blaimer & Fisher, 2016)
Erromyrma	*Monomorium*		(Ramamonjisoa, Rasoamanana & Fisher, 2023)
Lepisiota	*Prenolepis*	*Plagiolepis*	(Gaudard et al., 2019)
Lioponera	*Cerapachys*		(Brady et al., 2014)
Ooceraea	*Cerapachys*		(Brady et al., 2014)
Parasyscia	*Cerapachys*		(Brady et al., 2014)
Parvaponera	*Cryptopone*		(Branstetter & Longino, 2019)

252

253   References for Table S3

254   Brady, S. G., Fisher, B. L., Schultz, T. R., & Ward, P. S. (2014). The rise of army ants

255   and their relatives: diversification of specialized predatory doryline ants. *BMC*

256   *Evolutionary Biology*, *14*(1), 1–14.

257   Branstetter, M. G., & Longino, J. T. (2019). Ultra-conserved element phylogenomics of

258   New World Ponera (Hymenoptera: Formicidae) illuminates the origin and

18

259   phylogeographic history of the endemic exotic ant Ponera exotica. *Insect*

260   *Systematics and Diversity*, *3*(2), 1

261   Gaudard, C. A., Robertson, M. P. & Bishop, T. R. (2019). Low levels of intraspecific trait

262   variation in a keystone invertebrate group. Oecologia, *190*, 725–735.

263   Ramamonjisoa, M. M., Rasoamanana, N., & Fisher, B. L. (2023).   Description of the

264   male of *Erromyrma* Bolton & Fisher, 2016 (Hymenoptera, Formicidae). *ZooKeys*,

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266   Sparks, K. S., Andersen, A. N., & Austin, A. D. (2019). A multi-gene phylogeny of

267   Australian *Monomorium* Mayr (Hymenoptera: Formicidae) results in reinterpretation

268   of the genus and resurrection of Chelaner Emery. *Invertebrate Systematics*, *33*(1),

269   225–236.

270   Ward, P. S., Blaimer, B. B., & Fisher, B. L. (2016). A revised phylogenetic classification

271   of the ant subfamily Formicinae (Hymenoptera: Formicidae), with resurrection of

272   the genera *Colobopsis* and *Dinomyrmex*. *Zootaxa*, *4072*(3), 343–357.

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275   Table S4. All species with at least one record of negative environmental or

276   socioeconomic impacts in Gruber et al. (2022). * are species included in the Global

277   Invasive Species Database (http://www.iucngisd.org/gisd/). Harmful species included in

278   our analyses are bolded.

Anoplolepis custodiens
Anoplolepis gracilipes
Azteca sericeasur
Brachyponera chinensis*
Camponotus conspicuus zonatus
Cardiocondyla wroughtonii
Cardiocondyla emeryi
Formica aquilonia
Formica paralugubris
Lasius neglectus*
Linepithema humile*
Monomorium floricola*
Monomorium monomorium
Monomorium pharaonis*
Myrmica rubra*
Nylanderia bourbonica
Nylanderia fulva
Ochetellus glaber
Plagiolepis alluaudi

Paratrechina longicornis*
Pheidole megacephala*
Pheidole radoszkowskii
Solenopsis geminate*
Solenopsis invicta*
Solenopsis papuana*
Solenopsis richteri*
Tapinoma melanocephalum*
Tapinoma sessile
Technomyrmex albipes*
Technomyrmex difficilis
Tetramorium bicarinatum
Tetramorium simillimum
Trichomyrmex destructor
Wasmannia auropunctata*

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280   Table S5. Determinants of the indoor status of non-native ants (n = 4,890). Significant

281   results are bolded.

Full model ($R^2_m = 0.45$, $R^2_c = 0.98$) *Indoor.status~Native.Temp.PCA1*Introduced.Temp.PCA1+Native.Water.PCA1*Introdced.Water.PCA1+year+strata+(Introduced.Water.PCA1||species)+(Native.Temp.PCA1+Native.Water.PCA1||region)*			
	Chisq	Df	*p*-value
Introduced water PCA1	2.902	1	0.088
Native water PCA1	0.001	1	0.971
Introduced temperature PCA1	**12.426**	**1**	**<0.001**
Native temperature PCA1	0.518	1	0.472
Log10(date)	0.358	1	0.55
Strata	4.83	5	0.437
Introduced water PCA1 * Native water PCA1	0.037	1	0.847
Introduced temperature PCA1 * Native temperature PCA1	**18.878**	**1**	**<0.001**
Simplified model ($R^2_m = 0.45$, $R^2_c = 0.98$) *Indoor.status~Native.Temp.PCA1*Introduced.Temp.PCA1+Native.Water.PCA1*Introdced.Water.PCA1+year+strata+(Introduced.Water.PCA1||species)+(Native.Temp.PCA1+Native.Water.PCA1||region)*			

Introduced water PCA1	2.994	1	0.084
Native water PCA1	0.001	1	0.971
Introduced temperature PCA1	**12.626**	**1**	**<0.001**
Native temperature PCA1	0.493	1	0.482
Log10(date)	0.359	1	0.549
Strata	4.857	5	0.434
Introduced temperature PCA1 * Native temperature PCA1	**19.165**	**1**	**<0.001**
Final model ($R^2_m = 0.52$, $R^2_c = 0.94$) *Indoor.status~Native.Temp.PCA1*Introduced.Temp.PCA1+year+strata+(1|species)+(Native.Temp.PCA1||region)*			
Introduced temperature PCA1	**70.157**	**1**	**<0.001**
Native temperature PCA1	**11.789**	**1**	**0.001**
Introduced temperature PCA1 * Native temperature PCA1	**32.137**	**1**	**<0.001**

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284 Table S6. Determinants of the indoor status of non-native ants, after excluding potentially

285 undersampled regions based on three thresholds. Models are specified as the final model

286 in Table S3.

Excluding regions with no indoor non-native populations (n=1,411; R^2_m=0.38, R^2_c=0.84)			
	Chisq	Df	P-values
Introduced temperature PCA1	**39.999**	**1**	**<0.001**
Native temperature PCA1	**23.757**	**1**	**<0.001**
Introduced temperature PCA1 * Native temperature PCA1	**20.208**	**1**	**<0.001**
Excluding regions with ≤ 1 indoor non-native populations (n=776; R^2_m=0.36, R^2_c=0.87)			
Introduced temperature PCA1	**4.649**	**1**	**0.031**
Native temperature PCA1	**22.437**	**1**	**<0.001**
Introduced temperature PCA1 * Native temperature PCA1	**12.227**	**1**	**<0.001**
Excluding regions with ≤ 2 indoor non-native populations (n=597; R^2_m=0.43, R^2_c=0.87)			
Introduced temperature PCA1	2.58	1	0.108
Native temperature PCA1	**23.5**	**1**	**<0.001**
Introduced temperature PCA1 * Native temperature PCA1	**7.827**	**1**	**0.005**

287   Table S7. Percentage of climate change impacts associated with the top-10 and -20

288   countries under different scenarios. Climate change impacts are calculated as the sum of

289   gain in outdoor establishment probability.

2°C	Non-native	Harmful	Environmental	Socioeconomic
Top-10	68.2%	68.2%	83.9%	73.4%
Top-20	83.4%	87.9%	97.9%	93.3%
4°C	Non-native	Harmful	Environmental	Socioeconomic
Top-10	65.0%	64.3%	75.8%	63.8%
Top-20	84.6%	84.1%	96.5%	91.3%

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292　Table S8. Percentage of highly threatened countries scored as "comprehensive" in each

293　invasive species policy aspect.

2°C Non-native	Threat	List	Management	Research	Monitoring
Top-10	100	90	40	80	60
Top-20	100	85	30	80	65
4°C Non-native					
Top-10	100	90	30	90	70
Top-20	100	85	30	85	70
2°C Harmful					
Top-10	100	80	30	70	50
Top-20	100	85	30	75	60
4°C Harmful					
Top-10	100	90	40	80	60
Top-20	100	80	35	70	60
2°C Environmental					
Top-10	100	80	40	80	50
Top-20	100	85	30	85	60
4°C Environmental					
Top-10	100	80	40	80	60
Top-20	100	85	30	80	60
2°C Socioeconomic					
Top-10	100	90	40	70	70

Top-20	95	80	25	75	55
4°C Socioeconomic					
Top-10	100	80	50	80	60
Top-20	100	80	30	80	55

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