Diversity and Distributions

A Journal of Conservation 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: Thousands of non-native species have invaded outdoor environments, yet some

3   populations or species are confined indoors, potentially due to unsuitable climates. We

4   assessed the hypothesis that non-native species are more often restricted to indoor

5   environments when they invade regions with climates dissimilar from their native

6   distributions. Furthermore, we forecasted how climate change could influence the spread

7   of indoor non-native ant populations into outdoor environments and the associated

8   impacts.

9

10   Location: Global.

11

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

13   occurrences, we modelled how the confinement of non-native species to indoor settings

14   in regions was influenced by the regional climate, as well as the native climatic niches of

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

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

1

17 warming. We further evaluated how the anticipated increase in outdoor non-native ant

18 species would generate additional environmental and socioeconomic impacts using a

19 global dataset of 1,162 non-native ant impact records.

20

21 Results: Non-native ants from warm environments showed increased probabilities of

22 being restricted indoors when introduced to cold environments. Warming is projected to

23 reduce these restrictions, leading to an average increase of ~2% and ~8% in outdoor non-

24 native ant richness across regions globally under 2°C and 4°C of warming, respectively.

25 In regions where indoor environments contain non-native ants that can generate negative

26 socioeconomic and environmental impacts, their spread can exacerbate the potential

27 impacts of ant invasions by an average of ~6% and ~23% across regions under 2°C and

28 4°C of warming, respectively.

29

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

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

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

33 environments, with costly repercussions on nature and society.

34

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

36 matching, ants

2

37   **Introduction**

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

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

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

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

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

43   2017; Dawson et al., 2017; Lockwood, Cassey, & Blackburn, 2005). In contrast, the

44   factors influencing non-native species establishment in indoor environments, such as

45   buildings, stores, and greenhouses, and subsequent spread outdoors have been

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

47   environments to serve as invasion hotspots for many taxa (Donisthorpe, 1927; Wang,

48   Zhang, Pan, Li, & Zhu, 2015), such as terrestrial invertebrates (Kenis, Rabitsch, Auger-

49   Rozenberg, & Roques, 2007), plants (Van Kleunen et al., 2018), and fungi (Bradshaw et

50   al., 2022). In some regions, indoor environments contain as much as 71% of the total

51   non-native species richness of particular taxonomic groups (Roques et al., 2009). While

52   studies have discussed the factors facilitating the spread of non-native species from

53   indoor to outdoor environments (i.e., where their impacts pose a greater threat) (Ni &

54   Hulme, 2021; Wang et al., 2015), these effects can be difficult to assess due to a lack of

55   1) comprehensive data on non-native species residing indoors and 2) understanding of the

56   mechanisms determining the indoor and outdoor distributions of non-native species.

57   Similarities in the climatic conditions between the native distributions of non-native

58   species and their introduced regions are important predictors of establishment success,

59   known as climate matching (Richardson & Pyšek, 2012). It has been suggested that

3

60 indoor environments provide more suitable and stable microclimatic conditions to non-

61 native species compared with outdoor environments (Hulme, 2017; Wang et al., 2015).

62 Therefore, if non-native species are introduced to regions with climates dissimilar from

63 their native distributions, they could be restricted to indoor environments due to a lack of

64 suitable climatic conditions in outdoor environments. Additionally, climate change can

65 make outdoor climates more suitable for indoor non-native populations and release them

66 into outdoor environments (Hulme, 2017). This can subsequently amplify the burden of

67 biological invasions on ecosystems and societies, as some non-native species with indoor

68 populations are known to generate considerable environmental and socioeconomic

69 impacts when established in outdoor environments (Cannon, Matthews, & Collins, 2007).

70 In such a scenario, a country's capacity to prevent and control biological invasions

71 ("response capacity" hereafter) will be vital in determining the consequences of future

72 invasions under climate change (Early et al., 2016; Faulkner, Robertson, & Wilson,

73 2020). An important but unaddressed question is whether the anticipated spread of indoor

74 non-native populations to outdoor environments with climate change will concentrate in

75 countries with high response capacities, such that these emerging threats could be

76 contained or mitigated (Early et al., 2016; Faulkner et al., 2020).

77 Here, we use comprehensive distribution data of 323 non-native ant species (Guénard,

78 Weiser, Gómez, Narula, & Economo, 2017; Wong, Economo, & Guénard, 2023) to

79 assess how climatic conditions determine the indoor and outdoor distributions of non-

80 native ants globally. Ant invasions are known to generate high ecological and

81 socioeconomic impacts, with a recent conservative estimate suggesting that the

82 approximate economic cost of ant invasions has been at least US$51.93 billion globally

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83   since 1930 (Angulo et al., 2022; Gruber et al., 2022). While climate change is generally

84   thought to facilitate biological invasions, research has shown that the expected effects can

85   highly vary across non-native ant species (Bertelsmeier, Luque, Hoffmann, &

86   Courchamp, 2015).

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

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

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

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

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

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

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

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

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

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

97   high response capacity to biological invasions.

98

Methods

99   **Methods**

100   **Data sources**

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

102   descriptions are provided in Supporting Information Text S1).

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

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

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

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

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

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

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

110   (Figure 1; see Text S1 for a complete description of the database). Each occurrence record

111   was associated with a region. For each region, we followed the hierarchical classifications

112   of non-native ant species used in previous studies (Wong et al., 2023), with "Indoor"

113   referring to species with populations that were strictly restricted to indoor environments,

114   and "Naturalized" referring to species with populations that had established outdoors.

115   Hence, if a non-native species occupies indoor and outdoor environments in a given region,

116   it is classified as "Naturalized" but not "Indoor" for that region. Records known only from

117   quarantine facilities and thus indicative of transportation but not of establishment were

118   excluded. In total, the database identified 373 non-native ant species which were recorded

119   as "Indoor" or "Naturalized" in ≥1 region worldwide; these occurred in a total 5,176 non-

120   native and 12,353 native populations, respectively, with each population corresponding to

121   a unique record of a species in a region.

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

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

124   et al., 2022). The database contained 1,162 impact records of 100 species from 642

125   studies. We removed records indicating impacts unlikely to occur in outdoor

6

126   environments, such as food contamination, as our study is primarily interested in non-

127   native ants' impacts in outdoor environments. We extracted the impact scores of each ant

128   species associated with six categories of environmental impacts and six categories of

129   socioeconomic impacts.

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

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

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

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

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

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

136   subsequent model projections.

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

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

139   181 countries in 2015 based on their reports to the Convention of Biological Diversity

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

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

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

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

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

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

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

147   biological invasions relative to other countries.

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

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

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

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

152   shown that differences in socioeconomic conditions can be important determinants of

153   countries' response capacities (Latombe et al., 2023). These socioeconomic conditions in

154   2015 and 2021/2022 (the most updated data) exhibited strong positive correlations at

155   country levels (Pearsons's r > 0.88) (Table S1, Figure S2). Thus, the data should still

156   reflect the relative differences in response capacities between countries.

157

Climatic conditions in native and introduced environments

158

159   As the climatic variables were highly intercorrelated (R > 0.7 or < -0.7), we ran

160   separate PCAs for the variables associated with temperature and those associated with

161   water availability and extracted the scores of PCA1 in each analysis. The scores of PCA1

162   explained 76% and 62% of the global variation observed in climatic variables associated

163   with temperature and water availability, respectively (Table S2). We did not retain the

164   remaining PCA axes because their explanatory power was not significantly higher than

165   random. The significance test was based on the broken-stick criterion conducted in the R

166   package BiodiversityR (Kindt, 2023). To quantify native climatic niche, we extracted

167   PCA1 scores from each grid within the native distribution of each species and averaged

168   them to represent the climatic conditions in their native distribution. We also obtained

169   average PCA1 scores for each region in the introduced range.

8

170   Ideally, quantifying climatic niches should use occurrence data with high geographical

171   precision. Nevertheless, data sources providing detailed occurrence records, such as

172   GBIF, often have high geographical biases and misidentifications (Hughes et al., 2021).

173   Additionally, historical records (as early as 1793 in our database) can be important to

174   understanding invasion processes, yet these records often have higher positional

175   uncertainty. Therefore, we used occurrence data at regional levels for our studies, an

176   approach that has been employed in other niche modelling studies involving understudied

177   species (Fan et al., 2023).

178

Modelling indoor status

180   First, we designated the timing of the earliest record of a non-native species within a

181   region as its introduction year, which would be used to control propagule pressure

182   (Abellán et al., 2017). We excluded populations that had no dated records and 14 species

183   with no native distribution data available. These reduced the number of non-native

184   populations for subsequent analyses from 5,176 to 4,845.

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

186   region—was binary, we used generalized linear mixed models with binomial error

187   distributions to regress indoor status against the predictor variables (see Text S2 for

188   mathematic notations and R code). The model included records of all species from all

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

190   predictors included were the PCA1 of both the temperature and water variables in the

191   introduced and native range. In addition, we specified two two-way interaction terms in

9

192   the model: temperature PCA1 in the native distribution and the introduced region, and

193   water PCA1 in the native distribution and the introduced region. Inclusions of interaction

194   terms assess how climatic conditions in introduced regions filter species based on their

195   native distributions (ter Braak, 2019).

196   We additionally included covariates to isolate the effects of climatic drivers further.

197   First, we added the introduction year as a covariate to act as a proxy for propagule

198   pressure (Abellán et al., 2017). Introduction year was log-transformed to reduce

199   skewness. Second, we used data on the vertical habitat strata occupied by each non-native

200   ant species from Wong and colleagues (Wong et al., 2023), which indicated whether a

201   species was associated with the litter-and-soil, ground-surface, and/or arboreal strata In

202   total, there were six categories of vertical habitat strata ("litter-and-soil", "ground",

203   "arboreal", "ground and litter-and-soil", "ground and arboreal", "all").

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

205   intercepts. We also added climatic predictors as random slopes in the model, allowing

206   their effects to vary across polygons or species to minimize type-I error (ter Braak, 2019).

207   Introduction year and strata, however, were not added as random slopes to facilitate

208   model convergence, as they were not the primary interest of this study (Matuschek,

209   Kliegl, Vasishth, Baayen, & Bates, 2017).

210   The full model, however, resulted in singularity fits. Thus, we excluded temperature

211   PCA1 scores in the introduced regions from the random effects (but not fixed effects), as

212   its random-effect variance was close to zero. After assessing the statistical significance of

213   each term, we excluded any insignificant interaction terms and reassessed the

10

214   significance of the main effects (Schielzeth, 2010). If these main effects were still

215   insignificant, we removed them from the final model, which would be used for climate

216   change projections.

217   To ensure our models are robust, we assessed the extent of spatial and phylogenetic

218   autocorrelation in the residuals of the best model (Text S3, Table S3) and whether data

219   biases across regions could confound any climatic signals (Text S4).

220

Climate change projections

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

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

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

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

226   climatic conditions. Here, the goal is not to minimize the correlations between future

227   climatic variables but to convert them to scales comparable with the current climatic

228   variable and conduct climate change projections. Thus, we did not conduct another

229   separate PCA for future climatic variables.

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

231   for each introduced polygon. In the projections, we included all established populations

232   regardless of their indoor status and obtained naturalization probability for each

233   population. We calculated the effects of climate change on each population as differences

234   in their naturalization probability between future and current climates. Our projections

235   showed that naturalization probability was at most reduced by 0.1% and 0.5% across all

11

236   naturalized populations under 2°C and 4°C warming scenarios (n=4,334). Thus, in

237   subsequent analyses, we only considered changes in the naturalization probability for

238   indoor non-native populations (n=511).

239   We calculated the expected gain in naturalized non-native species by summing the

240   differences in naturalization probability between current and future scenarios across all

241   indoor non-native populations in each region. We also calculated the gain in "harmful"

242   species in each region by restricting the analyses to 32 ant species with negative

243   environmental or socioeconomic impact records in outdoor environments within their

244   non-native range (Table S4).

245   To examine how the naturalization of indoor harmful populations under climate

246   change could generate additional environmental and socioeconomic impacts in outdoor

247   environments, we calculated gains in cumulative impact scores of each region across all

248   indoor harmful populations between current and future climate scenarios. Specifically,

249   the differences in cumulative impact score in each region between future and current

250   climate were calculated as

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

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

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

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

255   socioeconomic impacts had six categories and were calculated separately, thus the

256   maximum number of j was 6. When there were multiple scores available for the same

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257   impact category, we used the maximum score for each species, a common approach in

258   invasive species risk assessments (Gruber et al., 2022). We assumed that the species had

259   no impact on the categories if no records were available.

260   Our results should not be interpreted as forecasts of the contributions of the spread of

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

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

263   identify the potential impacts often associated with indoor non-native ants benefiting

264   from climate change using impact scores. This approach is often used for spatial risk

265   assessment despite uncertainties in whether the potential impacts would be realized, as a

266   higher impact score indicates more potential impacts by non-native species, justifying the

267   prioritization of management (Katsanevakis, Tempera, & Teixeira, 2016).

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

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

270   conditions by summing impact scores across each naturalized harmful species in each

271   region, with their naturalization probability set as one. The impacts of all indoor

272   populations in outdoor environments were set to zero. We also calculated the sum of

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

274   change to better understand the primary mechanisms driving increased socioeconomic

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

276   environmental and socioeconomic impact scores across all indoor populations globally

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

278   future impacts.

279

Response capacity analyses

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

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

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

284   region with the largest gain in naturalization probability to represent each species in each

285   country (see Text S5 for details). Since we were primarily interested in the threats posed

286   by indoor populations, we only included countries (n = 54) with ≥ 1 indoor population

287   and response capacity data available for the analyses.

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

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

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

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

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

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

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

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

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

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

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14

299 **Results**

300 We analyzed 4,334 naturalized and 511 indoor populations. Our dataset included 323

301 species from 75 genera distributed over 479 regions (Figure 1). A total of 139 populations

302 of 41 non-native ant species had both indoor and outdoor records in a region, and 48 of

303 them were first detected indoors. Globally, European and North American regions had the

304 highest number of indoor non-native populations, with the highest number recorded in the

305 UK, where 53 of the 61 non-native species with established populations were restricted

306 indoors (Fig. 1a). Florida recorded the highest number of naturalized non-native ant species

307 (68 species naturalized; 0 species indoors) (Fig. 1b). There was a negative correlation

308 between indoor and naturalized non-native ant richness (Kendall's tau = -0.21).

309   Of the 323 non-native ant species analyzed, 32 species were considered harmful to the

310 environments or humans in outdoor environments (Table S3). Sixteen of these 32 harmful

311 non-native species had populations confined to indoor environments in at least one region,

312 with a total of 181 indoor populations. Of the 546 regions analyzed, a total of 142 and 76

313 regions had $\geq$ 1 indoor non-native and harmful ant populations. European and North

314 American regions had the highest number of indoor harmful ant populations (Fig. 1c), but

315 not naturalized harmful ant populations (Fig. 1d).

316   The UK exhibited the highest cumulative environmental (score=60; Fig. 1e) and

317 socioeconomic (score=38; Fig. 1g) impact scores across all indoor non-native ant

318 populations, while Queensland exhibited the highest cumulative environmental (score=114)

15

319   and socioeconomic impact scores (score=73) across all outdoor non-native ant populations

320   (Fig. 1f, 1h).

321

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

323   Using mixed-effects logistic regressions, we found that ant species originating from

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

325   indoors when introduced to relatively colder environments with a higher temperature

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

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

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

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

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

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

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

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

334   final model. Excluding potentially undersampled regions did not alter the conclusion that

335   non-native ants from warm environments have a higher probability of being restricted to

336   indoor environments compared with non-native ants from cold environments when

337   invading a cold region (Text S4, Table S6).

338

16

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

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

341 average probability for 511 indoor non-native populations of 113 species to spread into

342 outdoor environments under the 2°C and 4°C warming scenario increased by 3.6% (range

343 = 0–24.7%) and 14.2% (0–66.2%), respectively. We recorded similar increases for the

344 181 indoor populations of 16 harmful species analyzed, with the average probability

345 increased by 4.5% (0 – 24.7%) and 18.0% under the 2°C and 4°C (0–66.5%) warming

346 scenario, respectively.

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

348 harmful species within regions through the spread of indoor populations was 2.1% (mean

349 species gain = 0.1; range = 0–1.5) and 6.2% (mean = 0.1; range = 0–0.5), respectively

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

351 harmful species richness could be as high as 66.1% and 37.6% respectively, indicating

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

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

354 (average = 0.5; range = 0–5.2) and the latter increasing by 24.7% (average = 0.4; range =

355 0–1.5) on average. Again, we observed high spatial variation in the relative increases

356 across regions, with the number as high as 252.9% and 121.4% for non-native and

357 harmful species richness, respectively.

358

17

Potential impacts by indoor non-native ants under climate change

359   In both warming scenarios, we found that 73 of the 76 regions having ≥ 1 indoor

360   harmful population currently would have increased environmental impact scores in

361   outdoor environments, while 72 regions would have increased socioeconomic impact

362   scores. Impacts on plants (44 regions), animals (42 regions) and enhanced competition

363   (68 regions) would be the most prevalent environmental impacts associated with the

364   anticipated naturalization of populations of harmful species currently residing indoors,

365   while crop loss (64 regions), animal production (53 regions), and infrastructure (49

366   regions) would be the most prevalent socioeconomic impacts (Figure S3). The enhanced

367   environmental impacts would be strongly driven by the spread of indoor populations of

368   *Linepithema humile* (Figure S4). Alternatively, *L. humile*, *Hypoponera punctatissima*,

369   and *Paratrechina longicornis* would be the key species leading to increased

370   socioeconomic impacts under warming (Figure S4).

371   Under 2°C and 4°C warming, the average increases in environmental impact scores

372   across the 76 analyzed regions were 5.7% (mean score increase = 0.6; range= 0-4.1) and

373   22.5% (mean = 2.5; range = 0-11.8), but maximum increases could reach 31.6% and

374   140.3%, respectively (Figure 3e-f). Socioeconomic impact scores within regions would

375   also be increased by 6.0% (mean = 0.4; range = 0-2.5) and 23.8% (mean = 1.6; range = 0-

376   6.9) on average under 2°C and 4°C warming, but maximum increases could reach 62.0%

377   and 173.0%, respectively (Figure 3g-h).

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

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

18

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

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

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

382 Finland (Figure 3, Figure S5). We detected strong correlations between the two future

383 climate scenarios in their projected gains in non-native and harmful species richness,

384 environmental impacts, and socioeconomic impacts (Kendall's tau > 0.76). Limiting

385 warming to 2°C would reduce gain in naturalized non-native and harmful ant species

386 richness and the associated impacts, with the reduction being more prominent in

387 European regions and the USA (Figure S5).

388

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

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

391 highly heterogeneous at the country level (Figure S6). In both warming scenarios, the top

392 10 countries were associated with > 60.8% of climate change effects, while the top 20

393 were associated with > 83.5% (Table S7). We recorded minimal effects in countries that

394 had a total response capacity score < 2.5 (Figure S7). Less than 28.3% of effects would

395 occur in countries with a comprehensive response capacity in all aspects (i.e., Total score

396 = 5). Instead, most effects would be associated with countries that had a total score

397 ranging from 3-4 (Figure S7).

398   Of the top 20 countries predicted to suffer the strongest effects from the

399 naturalization of indoor populations with climate change, all except Luxembourg

400 recognized the threats of invasive species, and > 80 % had developed a comprehensive

401 list of current or potential invasive species (Figure S8, Table S8). We detected the

402 greatest shortfall in managing biological invasions (e.g., policies, legislations, and

19

403 resources that target problematic invasive species nationally), followed by monitoring

404 (e.g., facilities to report biological invasions, disseminating resources for identifying

405 invaders) among the highly threatened countries. Depending on warming scenarios and

406 the exact effects, only 25– 30% of the 20 most threatened countries had "comprehensive"

407 invasive species management, while 55 – 70% had established monitoring schemes, and

408 70 – 85% had existing research on invasive species. We obtained similar conclusions

409 when evaluating the top 10 countries only.

410

411 **Discussion**

412 We examined how outdoor climatic conditions can restrict non-native ants into indoor

413 environments, as well as the potential consequences of climate change on ant invasions

414 globally. Our findings from a global analysis of 323 non-native ant species broadly

415 demonstrate that indoor environments serve as unique microclimatic beachheads for non-

416 native ants from warm and aseasonal regions to bypass macroclimatic filters posed by

417 low and seasonal temperatures. Our global findings expand on previous studies focused

418 on individual regions and species (Hulme, 2017; Ni & Hulme, 2021; Wang et al., 2015).

419 Additionally, our results suggest that global warming will erode macroclimatic filters and

420 facilitate the naturalization of non-native ant populations that are currently confined to

421 indoor settings, including species that cause negative impacts. Moreover, we found that

422 the naturalization of indoor non-native populations with climate warming is more likely

423 to occur in regions lacking comprehensive capacities to manage and monitor biological

424 invasions. Altogether, these findings highlight the role of indoor populations in

20

425 exacerbating non-native ant invasions globally under climate change, which is unlikely to

426 be contained by current invasive species management, adding to the already high

427 negative impacts generated by invading ants (Angulo et al., 2022; Gruber et al., 2022).

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

429 2012), as increasing climatic similarities between native range and invaded regions were

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

431 temperature seasonality only. In fact, our database has few records of indoor non-native

432 populations in warm environments with a low temperature seasonality, in contrast to their

433 preponderance in cold environments with a high temperature seasonality. As with most

434 macroecological studies, we cannot entirely rule out the effects that geographic biases in

435 sampling efforts worldwide have had on the patterns observed (Hughes et al., 2021).

436 Nevertheless, we re-analyzed our data by excluding potentially undersampled regions and

437 obtained similar results (Table S6). Thus, we believe that our results reflect ecological

438 processes rather than sampling biases, at least for temperate regions, which are

439 overrepresented in our analyses after excluding undersampled regions. Our interpretation

440 is further supported by physiological studies showing that the average critical minimum

441 thermal limit of ant species lies at 5°C (Nascimento, Câmara, & Arnan, 2022), which is

442 often exceeded in the winter of temperate environments (Abatzoglou et al., 2018). In

443 contrast with cold regions, all non-native ant species had a high probability of

444 establishing in warm regions. One explanation is that air and soil temperatures at regional

445 levels rarely exceed the average critical maximum thermal limit for ants, which lies at

446 46°C (Nascimento et al., 2022). Nevertheless, heat stress in warm regions can still cause

447 substantial lethal and sublethal effects on ants (Leong, Hui, & Guénard, 2023). Unlike

21

448 lethal effects, sublethal effects might not act to restrict non-native ant species to indoor

449 environments, but increase their associations with such environments.

450   Since indoor environments help non-native species escape from cold stress, warmer

451 buildings can be expected to be more important in driving invasion. Microclimatic

452 conditions in indoor environments are influenced by building designs, uses, and human

453 behaviors, including wall thickness, the frequency and consistency of temperature

454 controllers use, and their effectiveness (Zhang & Yoshino, 2010). Apart from having a

455 suitable microclimate, indoor environments with high food and nesting site availability,

456 such as residential buildings and warehouses, can particularly favor ant invasions (Drees

457 & Summerlin, 1998). Alternatively, indoor environments such as greenhouses can have

458 enhanced food availability to ants due to the persistence of other insect pests (e.g., sap-

459 feeding hemipterans) and the release of biological controls (Blatrix, Colin, Wegnez,

460 Galkowski, & Geniez, 2018). Indoor environments can also support fewer invertebrate

461 and vertebrate predators of ants, especially those with large body sizes, leading to

462 releases from natural enemies (Keane & Crawley, 2002). These unique features could

463 make indoor environments easily invaded, especially if non-native ants are able to

464 naturalize, which would facilitate their dispersal and ultimately increase establishments

465 and negative impacts in other indoor environments, a phenomenon that has been observed

466 in other greenhouse pests such as moths (Messelink, Lambion, Janssen, & van Rijn,

467 2021).

468   As climatic conditions in indoor and outdoor environments can strongly differ,

469 indoor records should be excluded from distributional data if studies are primarily

22

470   interested in assessing the risks of outdoor environments to biological invasions or how

471   species expand their niche through invasions. Popular sources of distributional data, such

472   as GBIF, can contain indoor records, and previous studies do not always remove these

473   observations before analyses (Arnan et al., 2021). Climatic niche and species' abilities to

474   establish under novel climates can be overestimated if indoor records are included,

475   subsequently leading to erroneous risk assessments on sites susceptible to invasions and

476   species likely to become invasive (Soley-Guardia et al., 2016). Including indoor records

477   can also influence conclusions of processes driving invasion patterns, such as reducing

478   the importance of climatic variables due to the lack of macroclimatic filters in indoor

479   environments, and increasing the importance of propagule pressure (Lockwood et al.,

480   2005), potentially misleading management practices.

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

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

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

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

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

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

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

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

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

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

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

23

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

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

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

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

496   (i.e., excluding species that are pets and restricted within terrariums). We did not seek to

497   undertake a comprehensive assessment of the effects of climatic drivers on biological

498   invasions, as this would require information on failed establishment events following

499   introductions, for which data are presently unavailable. As our results do not capture the

500   full effects of climatic drivers on biological invasions or other invasion pathways, our

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

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

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

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

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

506   species residing indoors (Hulme, 2017).

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

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

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

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

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

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

513   4°C warming compared with the 2°C warming scenario. Although our analyses are

24

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

515   richness indoors (Bradshaw et al., 2022; Roques et al., 2009; Van Kleunen et al., 2018).

516   Managing the extent of warming could be key in limiting impacts contributed by the

517   spread of indoor non-native populations to outdoor environments. Failure to limit

518   warming would require strengthening response capacities, especially in the management

519   and monitoring of non-native species, to minimize the impacts of these anticipated

520   invasions.

521

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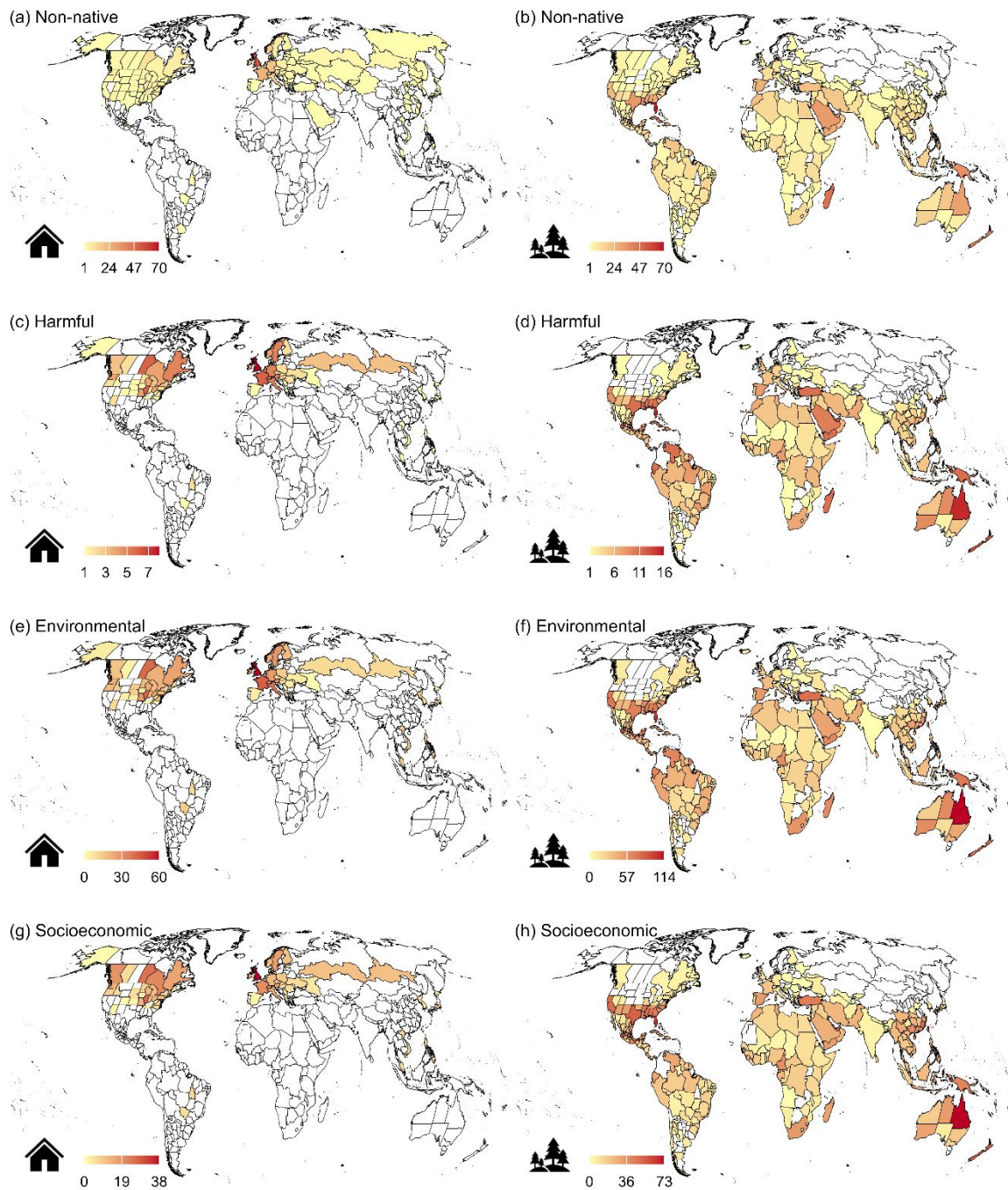
Figure 1. Global distribution of non-native (a,b) and harmful (c,d) ant species richness

used in the analyses, as well as their cumulative environmental (e,f) and socioeconomic

impact scores (g,h) of all harmful non-native species in indoor (a,c,e,g) and outdoor

655　environments (b,d,f,h). Populations without dated records and species without native

656　distribution data were excluded, which only represents ~5% of the data. Regions in white

657　lack records for non-native (a,b) and harmful (c-h) ant species established in indoor and

658　outdoor environments. Higher values in panel e-h indicate higher potential impacts of

659　harmful ants. As we only considered impacts in outdoor environments, panel e and g

660　reflect the potential of additional impacts if all the indoor ants spread into outdoor

661　environments.

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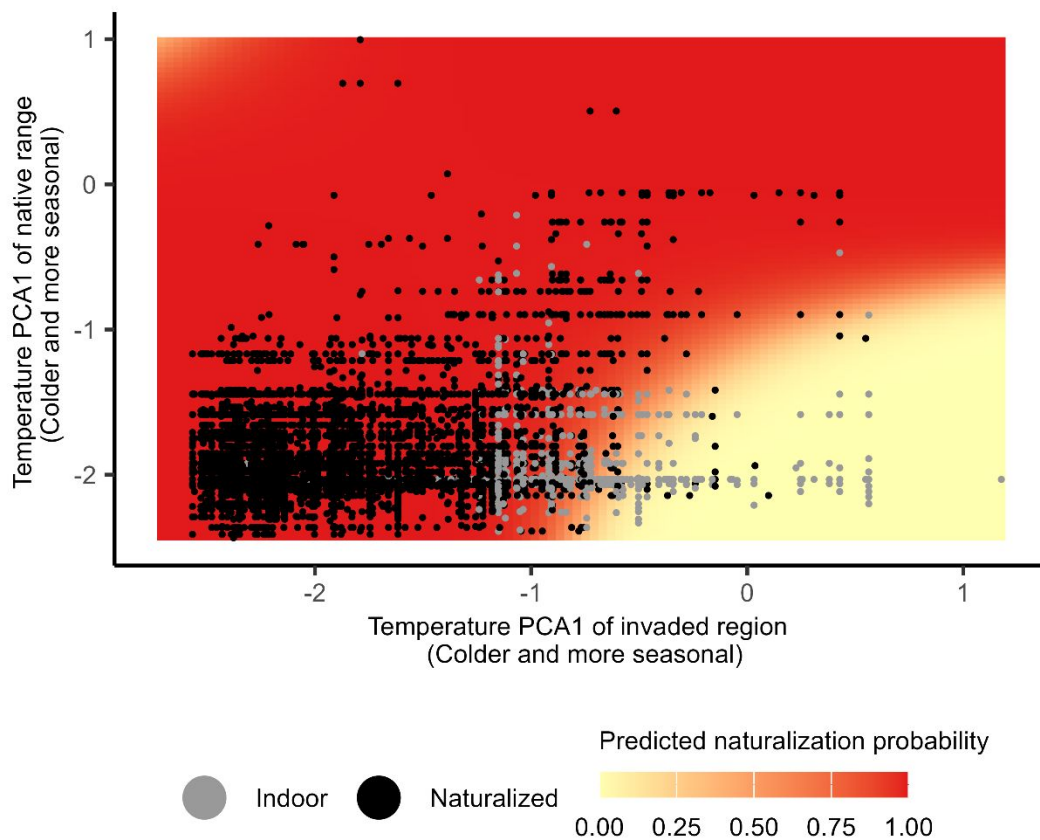
Figure 2. Differences between non-native ant species with naturalized (black dots) and indoor-confined (grey dots) populations in terms of the temperature and seasonality of their native and non-native ranges. Species originating from cold environments have a higher probability of establishing outdoors (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

674 region, with grey and black colours representing establishments in indoor and outdoor

675 environments, respectively. Increasing PCA1 scores along both axes indicate colder and

676 more seasonal temperature regimes, with Y-axis and X-axis indicating the climate in the

677 native range of each species, and the climate in the invaded region of each population,

678 respectively. Predicted naturalization probabilities are based on the fixed (but not
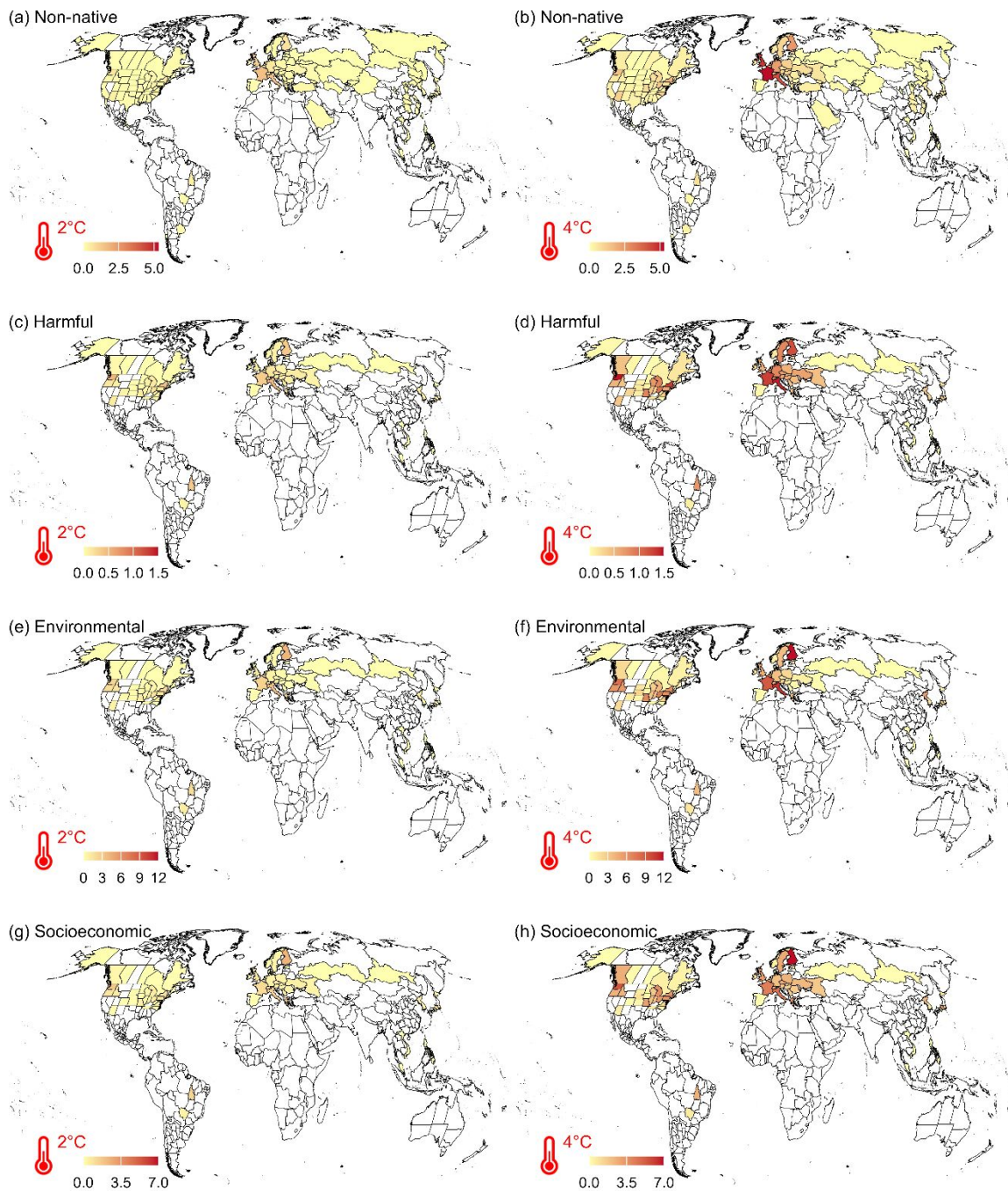
679 random) effects of the full model.

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681

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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 lack indoor non-native (a,b) and harmful

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

687   model.

37

Supporting Information for "Climate change can exacerbate ant invasion impacts by unleashing indoor populations into outdoor environments"

1 **Data availability statement**

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

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

4 695D/README.md. The finalized version will be uploaded to Github and Zenodo after

5 acceptance.

1

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

7   **Non-native ant records**

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

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

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

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

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

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

14   546 polygons was used for analyses, where an occurrence record could correspond to

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

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

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

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

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

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

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

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

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

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

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

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

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

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

2

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

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

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

32   records had conflicting statuses.

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

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

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

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

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

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

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

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

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

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

43

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

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

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

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

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

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

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

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

3

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

4

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

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

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

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

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

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

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

82

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

5

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

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

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

101   0.91). We included the 2°C and 4°C warming scenarios, with the former representing the

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

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

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

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

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

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

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

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

110   2023). Increasing PCA1 scores for all temperature variables indicated cooler and more

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

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

113   conditions to obtain future PCA1 scores of each grid.

114

115   **Response capacity**

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

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

118   countries' reports to the Convention of Biological Diversity

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

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

121   were available for these regions.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

7

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

143   invasive species management in highly threatened countries.

144

145   **References for Text S1**

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

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

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150   pathogenic and potentially pathogenic bacteria. *BMC Research Notes*, *12*, 1–5.

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152   native invasive plants in China. *Environmental Science & Technology*, *47*(14),

153   7624–7632.

154   Early, R., Bradley, B. A., Dukes, J. S., Lawler, J. J., Olden, J. D., Blumenthal, D. M.,

155   Gonzalez, P., Grosholz, E. D., Ibañez, I., & Miller, L. P. (2016). Global threats from

156   invasive non-native species in the twenty-first century and national response

157   capacities. *Nature Communications*, *7*(1), 12485.

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159   biosecurity is essential to prevent hundreds of harmful biological invasions. *Global

160   Change Biology*, *26*(4), 2449–2462.

161   Gruber, M. A. M., Santoro, D., Cooling, M., Lester, P. J., Hoffmann, B. D., Boser, C., &

162   Lach, L. (2022). A global review of socioeconomic and environmental impacts of

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

8

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

166   geographic distribution of ant species (Hymenoptera: Formicidae). *Myrmecological*

167   *News*, *24*, 83–89.

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169   species on marine ecosystems: the Mediterranean Sea case study. *Diversity and*

170   *Distributions*, *22*(6), 694–707.

171   Kindt, R. (2023). *BiodiversityR: Package for Community Ecology and Suitability*

172   *Analysis*. http://www.worldagroforestry.org/output/tree-diversity-analysis

173   Wong, M. K. L., Economo, E. P., & Guénard, B. (2023). The global spread and invasion

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

175

176

9

177   **Supporting Information Text S2 – Details of the full model**

178   We constructed a mixed-effect regression model with a binomial distribution to model

179   the indoor status of non-native ant populations of species j in region i. For the factor

180   "strata", we set "all" as the reference level. The full model was structured as follows:

$$log(P/(1-P)) = (\beta_0 + a_i + a_j) +$$

$$(\beta_1 + b_i)(Native.Temp.PCA1) + (\beta_2 + c_j)(Introduced.Temp.PCA1) +$$

$$(\beta_3 + d_i)(Native.Water.PCA1) + (\beta_4 + e_j)(Introduced.Water.PCA1) +$$

$$\beta_{12}(Native.Temp.PCA1 \times Introduced.Temp.PCA1) +$$

$$\beta_{34}(Native.Water.PCA1 \times Introduced.Water.PCA1) +$$

$$\beta_5(year) + \beta_6(Strata\_arboreal) + \beta_7(Strata\_ground) +$$

$$\beta_8(Strata\_litter\text{-}and\text{-}soil) + \beta_9(Strata\_ground\ and\ litter\text{-}and\text{-}soil) +$$

$$\beta_{10}(Strata\_ground\ and\ arboreal)$$

181   where P represents the probability of a non-native ant population being classified as

182   "Naturalized". All βs represent fixed effects, and $\times$s represent interaction terms. Random

183   effects are denoted in Latin. a_i and a_j represent the random intercepts with respect to

184   region and species identity, respectively. b_i and d_i represent regional differences in the

185   effect of temperature and water availability in native distribution of non-native ants in

186   determining naturalization probabilities. c_j and e_j represent species differences in the

187   effect of temperature and water availability in introduced regions in determining

188   naturalization probabilities. All random effects follow a normal distribution. We assumed

189   no correlation between the random intercepts and slopes.

190   In glmmTMB, the code to construct the full model is:

10

Indoor.status ~ Native.Temp.PCA1*Introduced.Temp.PCA1 +

Native.Water.PCA1*Introdced.Water.PCA1 + year + strata +

(Introduced.Temp.PCA1+Introduced.Water.PCA1||species) +

(Native.Temp.PCA1+Native.Water.PCA1||region)

191

192   Note that because of singular fits, *Introduced.Temp.PCA1* was subsequently dropped

193   from the model.

194

195   **Supporting Information Text S3 – Assessing autocorrelations**

196   To ensure our results were robust to spatial and phylogenetic autocorrelation, we

197   quantified Moran's I in the residuals of the final model. For spatial autocorrelation, the

198   distances between polygons were calculated based on their centroid. For phylogenetic

199   autocorrelation, we obtained phylogenetic distance from the genus-level phylogenetic

200   tree for ants (Economo, Narula, Friedman, Weiser & Guénard, 2018). After converting

201   the tree to ultrametric using UPGMA (Cophenetic correlation coefficient between the

202   unconverted and converted tree = 0.96), eight missing genera (11 % of total genera) were

203   placed as basal polytomies of their sister genus in the tree (Table S3). Autocorrelation

204   assessments were conducted using the R package *DHARMa* (Hartig, 2022).

205

206   Reference

207   Economo, E. P., Narula, N., Friedman, N. R., Weiser, M. D., & Guénard, B. (2018).

208   Macroecology and macroevolution of the latitudinal diversity gradient in ants.

209   *Nature Communications*, 9(1), 1778.

210   Hartig, F. (2022). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level /*

211   *Mixed) Regression Models*. https://CRAN.R-project.org/package=DHARMa

212

213

214 **Supporting Information Text S4 – Sensitivity analyses**

215   Data biases could affect our results by confounding the signals of climatic variables.

216 For instance, indoor environments in the tropics could be more undersampled compared

217 with temperate regions. These methodological biases could co-vary with climatic

218 gradients, which would lead to a pattern that most non-native ants are able to naturalize

219 under tropical climate. Unfortunately, quantifying the extent of undersampling in each

220 region would be impossible. Thus, we used the number of indoor populations as an

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

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

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

224 climatic effects but not sampling biases across climatic gradients.

225

226

13

227   **Supporting Information Text S5 – Upscaling regional impacts to the country levels**

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

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

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

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

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

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

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

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

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

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

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

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

240   country.

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

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

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

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

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

246   "Sudan", "Cyprus"), but they did not contain any indoor populations and therefore would
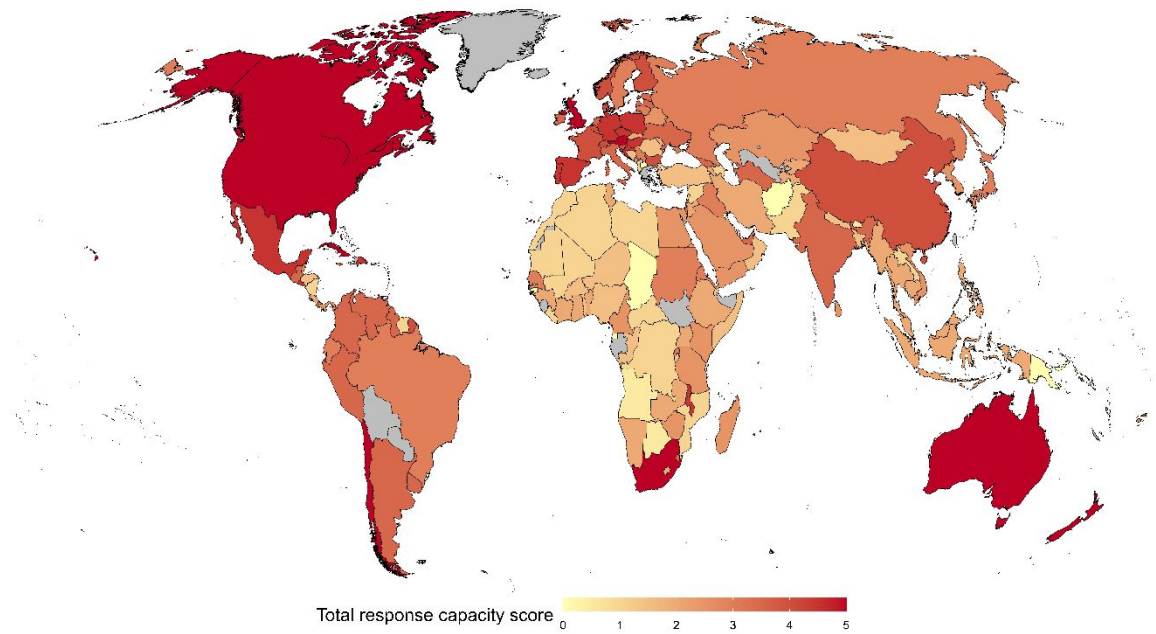
247   not affect the country-level analyses.

14

Total response capacity score

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

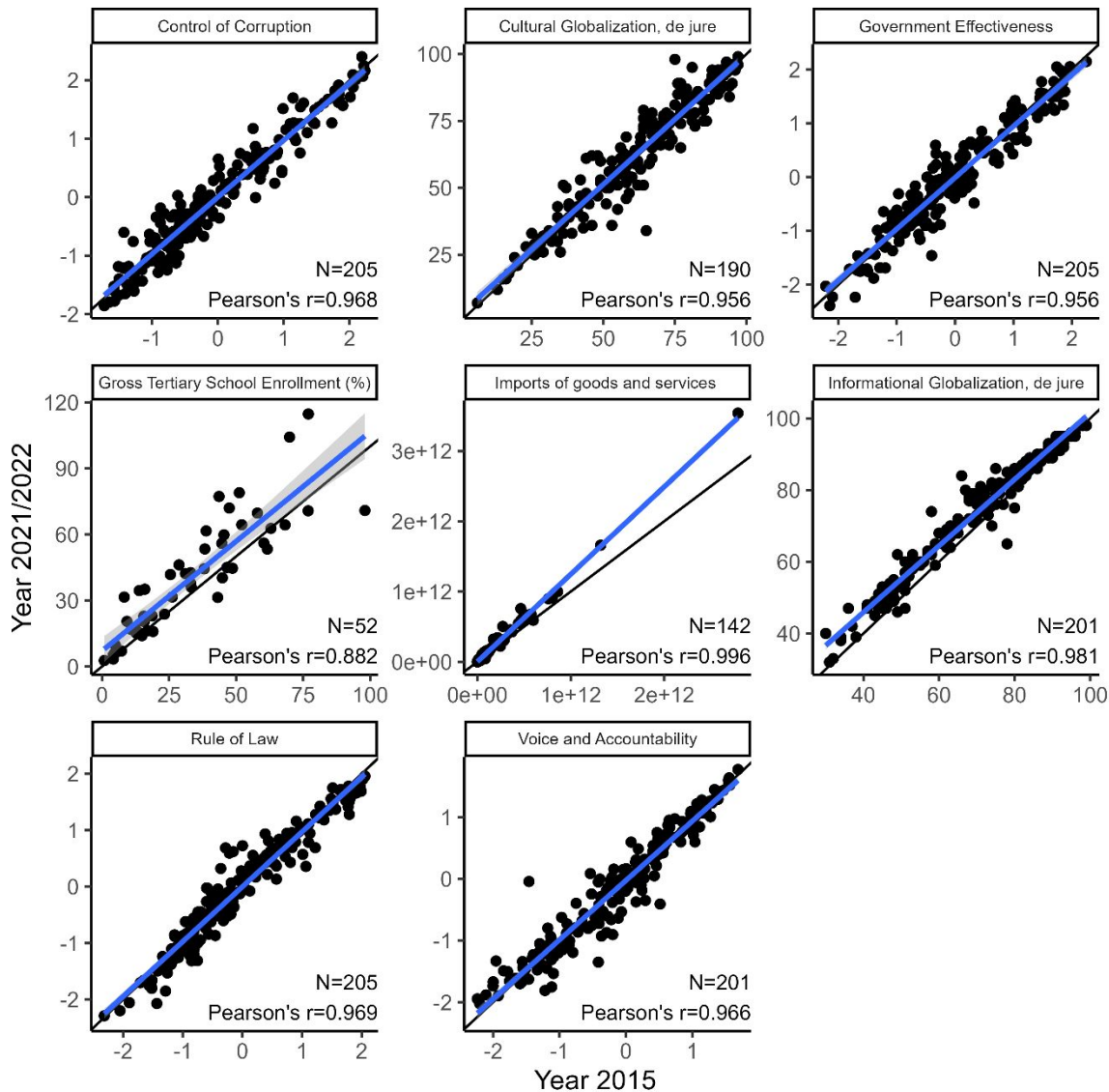251   (2016). Higher scores indicate better response capacity.

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.
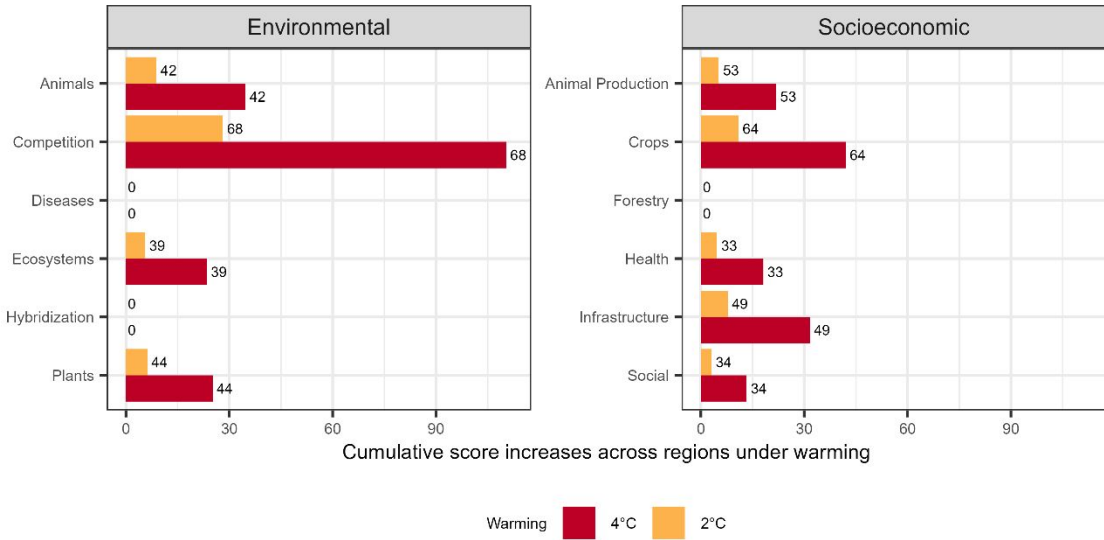
Figure S3. Cumulative score increases across regions for different impact categories under two warming scenarios. A higher increase in impact scores indicates the negative effects become stronger under warming. The number beside each bar represents the number of regions with increased impacts.
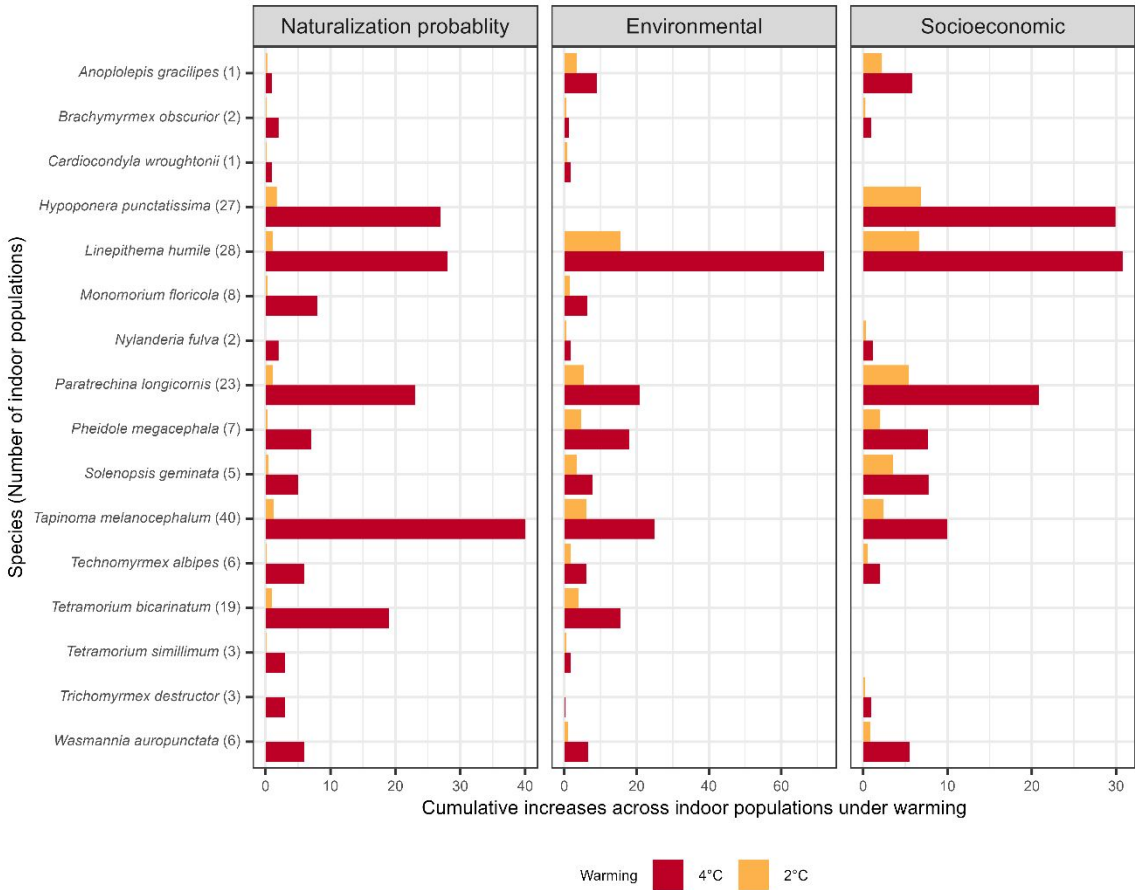
266

Figure S4. 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*,

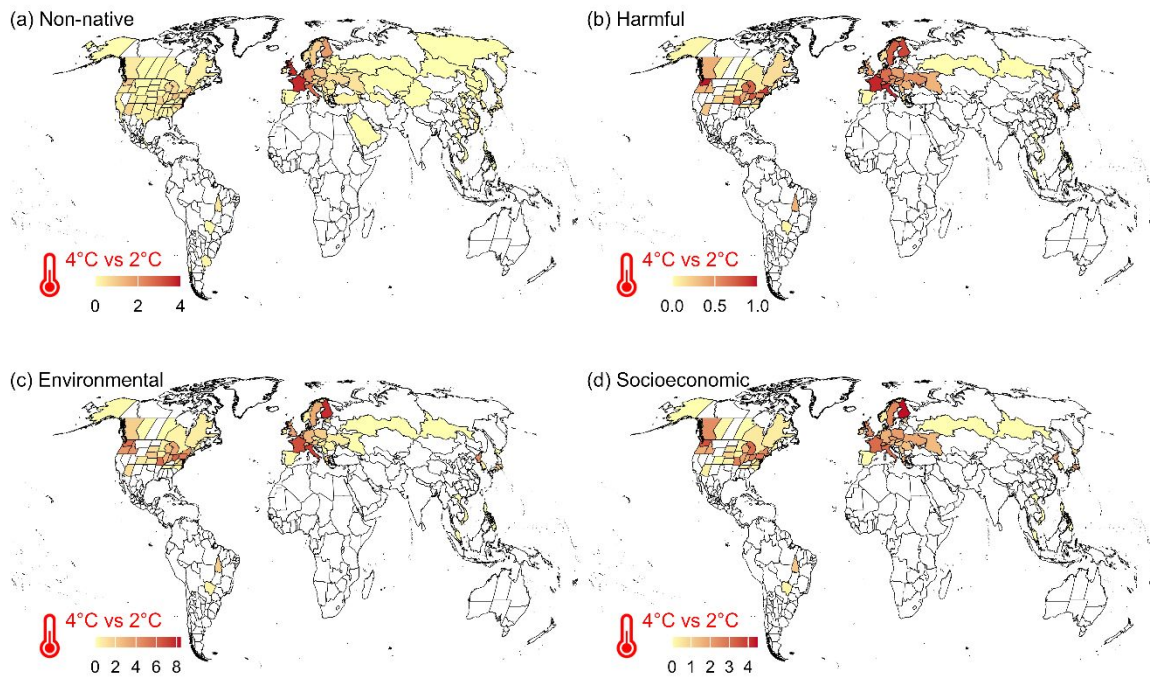*Brachyponera chinensis* are not shown here due to a lack of indoor record at present.

274

(a) Non-native

4°C vs 2°C
0   2   4

(b) Harmful

4°C vs 2°C
0.0   0.5   1.0

(c) Environmental

4°C vs 2°C
0 2 4 6 8

(d) Socioeconomic

4°C vs 2°C
0 1 2 3 4

275

276   **Figure S5.** Additional gains in non-native (a) and harmful species richness (b),

277   environmental impacts (c), and socioeconomic impacts (d) under 4°C warming compared

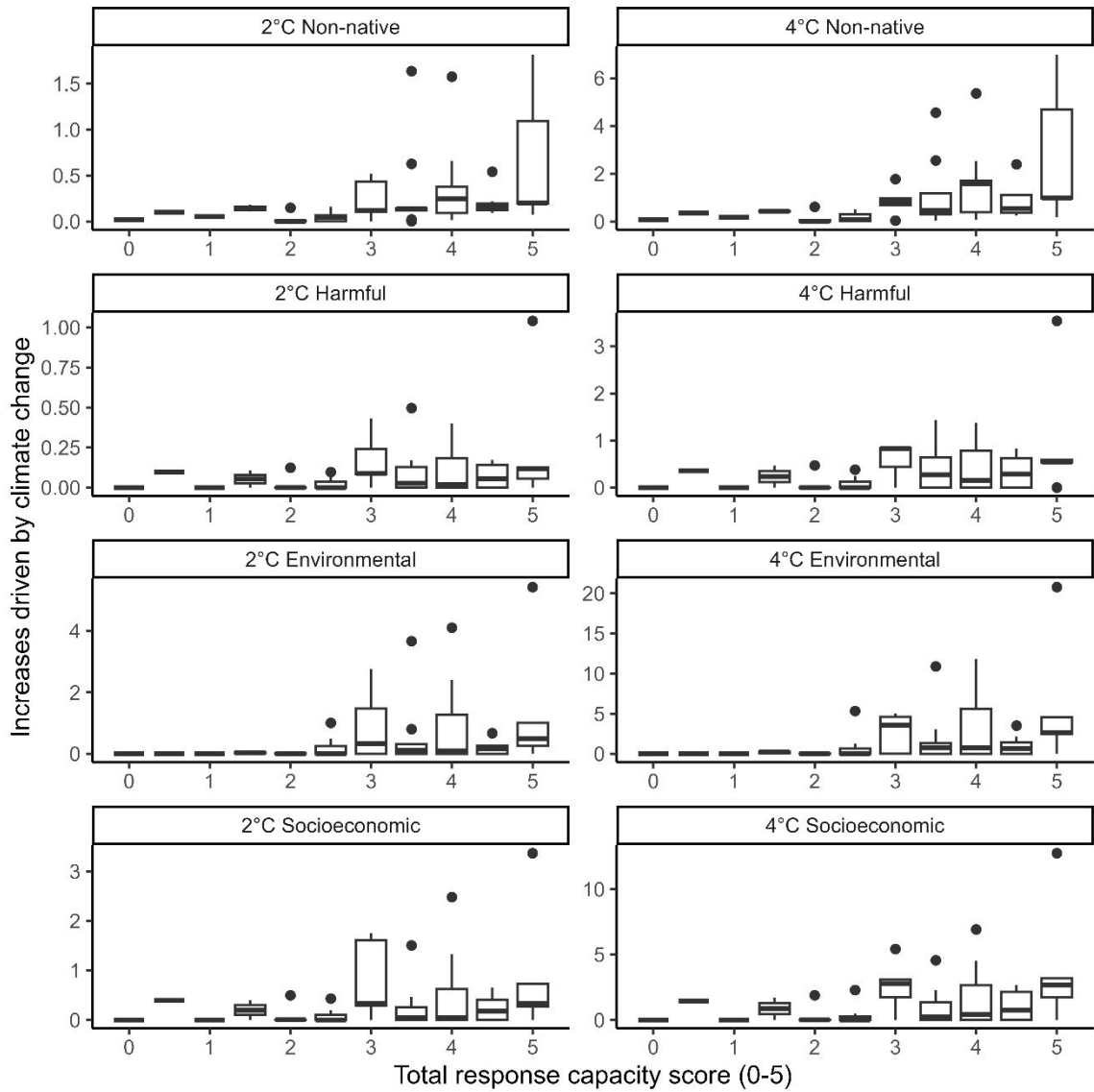278   to 2°C warming.

279

19

280

281 **Figure S6.** Climate change impacts across countries with different levels of response

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

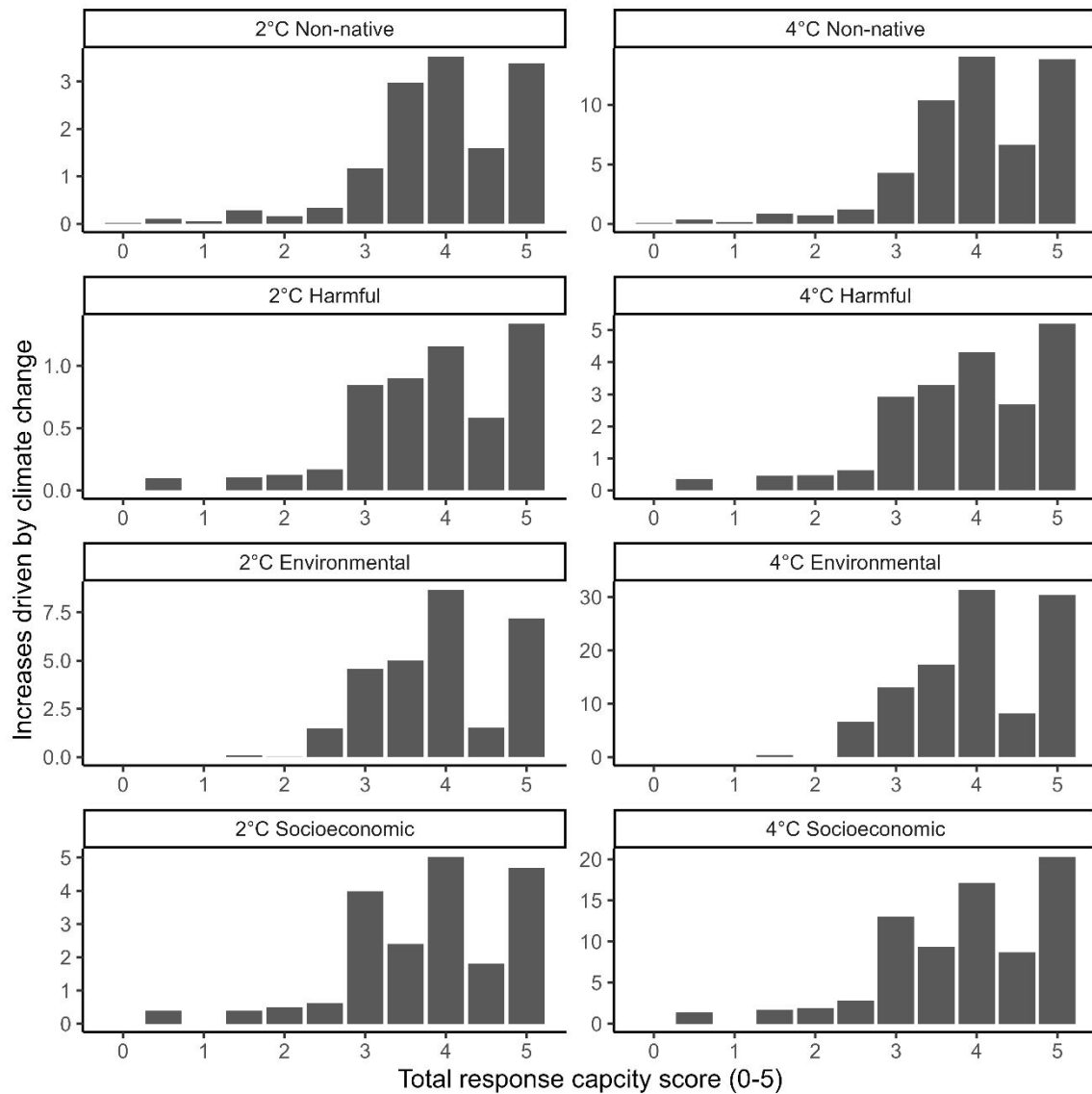283 naturalization probability.

284

20

Figure S7. The impacts of climate change in facilitating the spread of indoor non-native

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

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

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

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

21

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

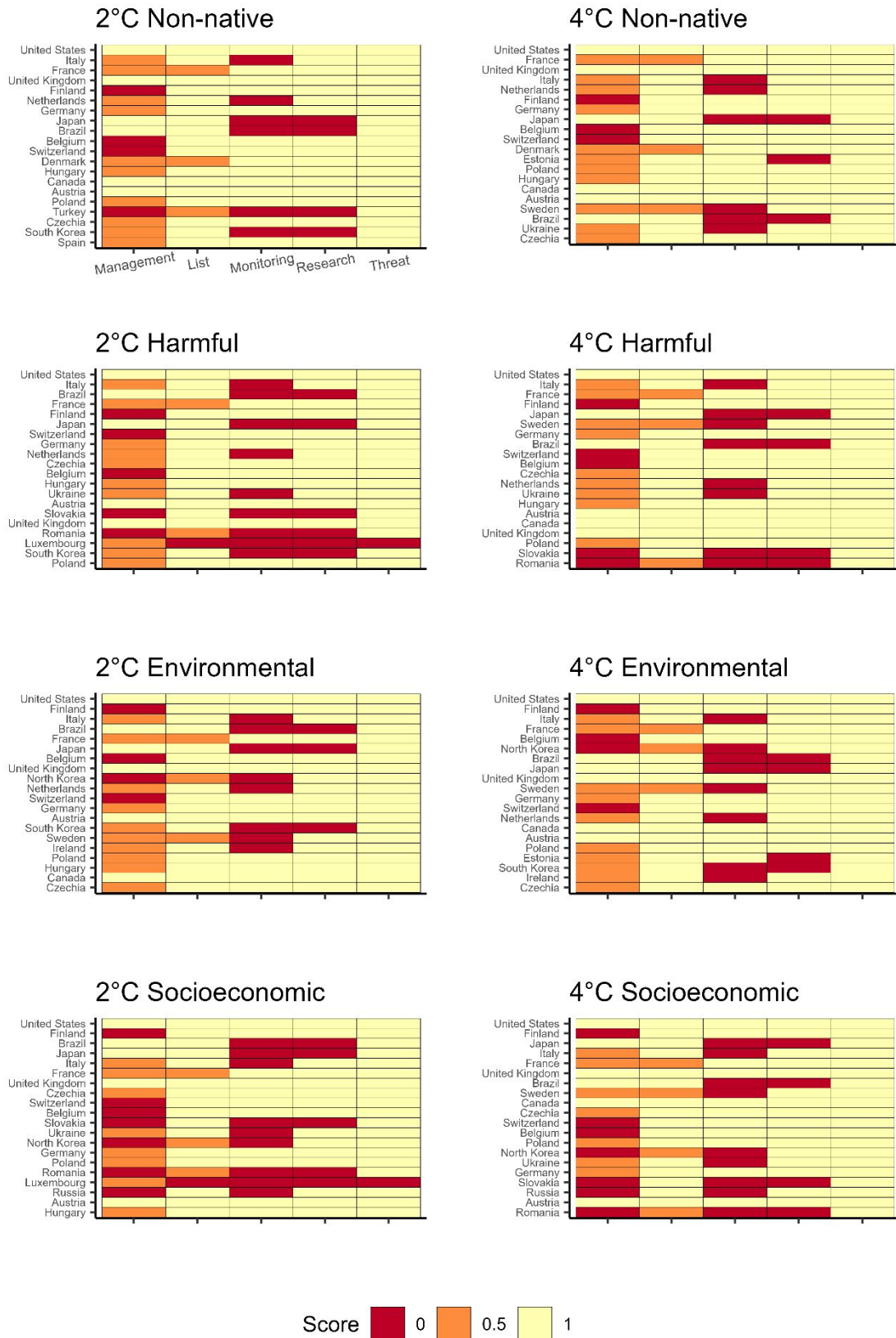292 more comprehensive policies on biological invasions.

293

22

Figure S8. Scores of response capacity in top-20 countries with the highest projected

23

296   gains in non-native or harmful species in outdoor environments under two warming

297   scenarios. Countries at the top of the y-axes are projected to experience the highest gains

298   in the species richness of non-native or harmful ants due to the anticipated spread of

299   indoor populations to outdoor environments under climate warming. A country with

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

24

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

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

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

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

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

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

307

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

25

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

308

309   References for Table S1

310   Dreher, A. (2006). Does globalization affect growth? Evidence from a new Index of

311   Globalization, *Applied Economics 38*, 10: 1091-1110.

312   Gygli, S., Haelg, F., Potrafke, N. & Sturm, J.-E. (2019). The KOF Globalisation Index –

313   Revisited, *Review of International Organizations, 14(3), 543-574*.

314   Latombe, G., Seebens, H., Lenzner, B., Courchamp, F., Dullinger, S., Golivets, M.,

315   Kühn, I., Leung, B., Roura-Pascual, N., & Cebrian, E. (2023). Capacity of countries

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

317   The World Bank (2024). World Development Indicator | DataBank.

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

319   2024-03-03.

320

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

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

323   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

324

27

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

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

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

328   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)

329

330   References for Table S3

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

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

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

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

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

28

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

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

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

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

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

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

342   *1163*, 61.

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

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

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

346   225–236.

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

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

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

350
351

352   Table S4. Species classified as harmful in our study. * are species with at least one indoor

353   population.

*Anoplolepis gracilipes**
*Brachymyrmex obscurior**
Brachyponera chinensis
Brachyponera sennaarensis
*Cardiocondyla wroughtonii**
Doleromyrma darwiniana
Formica paralugubris
*Hypoponera punctatissima**
Lasius neglectus
Lepisiota frauenfeldi
*Linepithema humile**
*Monomorium floricola**
Myrmica rubra
*Nylanderia fulva**
Nylanderia vaga
Odontomachus bauri
*Paratrechina longicornis**
*Pheidole megacephala**
*Solenopsis geminate**
Solenopsis invicta
Solenopsis papuana

30

Solenopsis richteri
Solenopsis saevissima
*Tapinoma melanocephalum**
Tapinoma nigerrimum
*Technomyrmex albipes**
Technomyrmex jocosus
*Tetramorium bicarinatum**
*Tetramorium simillimum**
Tetraponera rufonigra
*Trichomyrmex destructor**
*Wasmannia auropunctata**

354

31

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

356   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)			

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

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

360   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**

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

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

363   gain in outdoor establishment probability.

2°C	Non-native	Harmful	Environmental	Socioeconomic
Top-10	68.2%	69.2%	83.8%	73.4%
Top-20	83.5%	91.4%	97.8%	93.4%
4°C	Non-native	Harmful	Environmental	Socioeconomic
Top-10	65.0%	60.8%	75.7%	63.5%
Top-20	84.5%	88.9%	96.4%	91.3%

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

367   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	70
4°C Non-native					
Top-10	100	90	30	90	70
Top-20	100	85	30	85	70
2°C Harmful					
Top-10	100	90	30	80	60
Top-20	100	85	25	70	55
4°C Harmful					
Top-10	100	80	30	80	60
Top-20	100	85	30	80	60
2°C Environmental					
Top-10	100	80	40	80	50
Top-20	100	85	30	85	60
4°C Environmental					
Top-10	100	70	40	80	60
Top-20	100	85	30	80	60
2°C Socioeconomic					
Top-10	100	90	40	70	70

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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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