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

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This PDF file includes:

> Main Text
> Figures 1 to 4

1 **Abstract**
2 Thousands of alien species have successfully invaded outdoor environments, yet some
3 populations or species are confined indoors in their introduced range. It is generally assumed—
4 but rarely tested—that inhospitable climatic conditions of outdoor environments limit
5 establishments of these alien species outdoors. Here, we investigate whether climatic conditions
6 indeed restrict alien species to indoor environments. Furthermore, we examined how climate
7 change could influence the spread of indoor populations into outdoor environments, and
8 evaluated the capacities of different countries to manage alien ant invasions. Analyzing a global
9 dataset of ant species distributions of ~2.5 million occurrences, we found that alien ants from
10 warm environments with lower temperature seasonality showed increased probabilities of being
11 restricted indoors when introduced to cold environments with higher temperature seasonality.
12 Outdoor alien species and their associated environmental and socioeconomic impacts increased
13 an average of 2-3% across regions under 2°C warming, but elevated to 8-9% across regions
14 under 4°C warming. Regardless of warming scenarios, the anticipated spread of indoor alien
15 populations and their associated impacts would concentrate in European countries lacking
16 comprehensive management and monitoring schemes, such as France, Italy, and Finland.
17 Overall, our findings suggest that indoor environments serve as key microclimatic bridgeheads for
18 ant invasions, especially in cold and seasonal regions of the world. Failure to limit warming
19 extents in these regions could facilitate the spread of indoor alien ant populations into outdoor
20 environments, initiating new invasions and requiring costly management and mitigation efforts to
21 counter their impacts.

22

23 **Significance Statement**
24 Many species introduced to non-native regions by humans (i.e., alien species) are confined to
25 indoor environments. It is unclear whether climatic barriers presently limit their spread to outdoor
26 environments, and if future climate change will weaken such barriers. In a global analysis, we find
27 that cold regions with seasonal climates contain many indoor populations of alien ant species—
28 most originating from warmer, less seasonal climates. On average, the anticipated spread of
29 indoor alien populations under 2°C and 4°C warming would increase regional outdoor alien
30 species by 2-3% and 8-9%, respectively, with their associated impacts exhibiting similar trends.
31 Our findings highlight the need to limit warming extent and strengthen biological invasion
32 management to minimize impacts by indoor alien ants spreading outdoors.

33

Main Text

Introduction

To manage the impacts of biological invasions, numerous studies have identified invasion hotspots and the mechanisms determining invasion success in outdoor environments (1–4). Although indoor environments such as buildings, stores, and greenhouses have long been identified as invasion hotspots (5), the ecology of these environments and the species within them are understudied. Yet in some taxa and regions, as many as 71% of alien species are only recorded indoors (6–10). Some alien insects and plants have spread from indoor to outdoor environments (i.e., naturalize) or are expected to spread if they successfully escape (11–14), but other species may face barriers to naturalization. While many studies have highlighted the potential of indoor environments in increasing the spread and eventually impacts of alien species (7, 11, 14), their exact importance can be difficult to assess due to a lack of 1) comprehensive data on alien species residing indoors and 2) understanding of mechanisms determining alien species indoor and outdoor distributions.

Increased similarities in the climatic conditions between the native distributions of alien species and their introduced regions can facilitate establishments in a process known as climate matching (15). Inabilities to survive through cold winters are often believed to restrict alien species to indoor environments that harbor warmer or more stable microclimatic conditions (9, 11, 14, 16). This can be particularly true for species invading from warm regions, as they are not pre-adapted to the winter stress in outdoor environments (17). Theoretically, species invading from colder environments can also be restricted indoors in warmer regions, provided that these indoor environments have cooler microclimatic conditions than outdoor environments. Mismatches in other climatic conditions, including higher seasonality and precipitation, can also restrict alien species indoors, given their roles in shaping the diversity patterns of alien species (3, 18). Nevertheless, empirical tests on how climatic conditions determine alien species' indoor and outdoor distributions are rare and often based on limited taxonomic and spatial coverage (7, 11, 14), precluding generalizations on incompatible climates as a mechanism restricting alien species indoors.

If climatic conditions restrict alien ants indoors, the anticipated weakening of winter stress under climate change is expected to release indoor alien populations to invade outdoor environments, especially in European regions where many such indoor populations currently exist (7, 11, 16, 19). Some species are known to generate considerable environmental and socioeconomic impacts (20, 21), thus their spread from indoor to outdoor environments could lead to considerable negative impacts. If climate change makes outdoor conditions more climatically compatible for indoor alien populations, the capacity to prevent and control biological invasions ("response capacity" hereafter) will be vital in determining the consequences of future invasions under climate change (22, 23). Specifically, countries with a high response capacity can design and implement eradication, containment, or mitigation measures more effectively (22) to prevent or limit negative environmental and socioeconomic impacts of biological invasions in comparison with countries that have a low response capacity (24). Globally, response capacities to biological invasions are generally more comprehensive in developed countries than in developing countries, although comprehensive policies are still lacking in many developed countries (22). An important but unaddressed question is whether the anticipated spread of indoor alien populations under climate change would concentrate in countries with high response capacities, such that these emerging threats could be contained or mitigated (22, 23).

Ants represent an ideal system for investigating if climate has a generalizable role in restricting alien populations indoors, as at least 520 described ant species have been recorded outside of their native ranges globally, with comprehensive data documenting their indoor and outdoor distributions (19, 25). Furthermore, as introduction events for alien ants almost always occur by accident, the effects of ecological processes such as climate matching are likely to be more prominent in shaping their indoor and outdoor distributions than for intentionally introduced

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86   taxa (26, 27). Ant invasions are also known to generate high environmental and socioeconomic
87   impacts, making them important targets for alien species management. These include invasive
88   species such as *Solenopsis invicta* and *Linepithema humile* (21), as well as a variety of species
89   that have established alien populations in both indoor and outdoor environments, or exclusively in
90   indoor environments (19, 25, 28). If established in outdoor environments, alien ants can lead to
91   environmental impacts, such as reducing native arthropod diversity and abundance (29–32), and
92   affecting key ecosystem functions such as scavenging and seed dispersal (33, 34). Some ant
93   species also generate negative socioeconomic impacts in outdoor environments such as causing
94   crop loss, public health concerns by biting and stinging people, or disrupting educational
95   programs (21, 35, 36). A recent conservative estimate suggests that the economic cost of ant
96   invasions has approximated at least US$51.93 billion globally since 1930 (35). Nevertheless, the
97   expected responses of invasive ants to climate change are highly idiosyncratic (37), thus it is
98   unclear if changing climatic conditions will systemically facilitate the spread of indoor alien ant
99   populations outdoors. Currently, most recorded indoor populations of alien ants are located in
100   Europe and North America (Figure S1a,c), contrasting the distribution of alien ant diversity in
101   outdoor environments globally (Figure S1b,d) (18, 23). In indoor environments, alien ants can act
102   as domestic pests affecting human activities (18). For instance, some species pose a concern to
103   public health by attacking residents or carrying pathogens (38) while others inflict socioeconomic
104   damage by killing biocontrol agents in greenhouses (39).

105   Here we use comprehensive data on the native and non-native distributions of all known
106   alien ant species to assess how climatic conditions restrict their established populations to indoor
107   environments globally. In accordance with the climate matching hypothesis, we predicted that
108   alien ants invading regions with similar climatic conditions to their native distributions would have
109   increased success in establishing outdoor populations. We further examined how climate change
110   would affect the distributions of indoor and outdoor populations of different alien ant species, and
111   estimated the resultant changes in the richness of alien species in outdoor environments of
112   regions globally. Additionally, we examined how the anticipated spread of alien ants could
113   exacerbate their negative outdoor environmental and socioeconomic impacts in different regions
114   around the globe. Finally, to examine whether these potential invasions facilitated by climate
115   change would be effectively contained, we assessed whether they were concentrated in countries
116   with a comprehensive response capacity to biological invasions.

117

118   **Results**
119   Using the Global Ant Biodiversity Informatics (GABI), a database of 2.5 million ant occurrence
120   records (25), we extracted the indoor and outdoor (i.e. naturalized) status of each alien species in
121   each region. Regions were defined at country levels, or at lower administrative units for larger
122   countries such as China, Canada and the US. Some regions reflected natural boundaries such as
123   many island systems (Figure S1; see Text S1 for a complete description of the database). Each
124   occurrence record was associated with a region, and multiple records of the same alien species in
125   the same region were considered as the same population. Populations were considered "indoor" if
126   all records were from indoor environments such as greenhouses and residential buildings, while
127   populations with at least one outdoor record were considered "naturalized", even if there were
128   indoor records of the populations (19, 25).

129   We analyzed 4,316 naturalized and 503 indoor populations of alien ants globally. Our dataset
130   included 323 species from 75 genera distributed over 478 regions (Figure S1). Of these, 21 alien
131   ant species (Table S1), which had 298 indoor populations in our dataset, were considered harmful,
132   as these species had at least one negative environmental or socioeconomic impact record in a
133   recent impact assessment (21). A total of 133 populations had both indoor and outdoor records,
134   and 48 of them were first detected indoors. Globally, the region with the highest number of indoor
135   alien populations was the UK, where 51 of the 58 alien species with established populations were
136   restricted indoors. Florida recorded the highest number of naturalized alien ant species (68 species
137   naturalized; 0 species indoors). There was a weak negative correlation between indoor and

138   naturalized alien ant richness (Kendall's tau = -0.10). A total of 142 and 137 regions had ≥ 1 indoor
139   alien and harmful ant population, of which 33 (23.2%) and 50 (36.8%) currently had no naturalized
140   alien and harmful species, respectively.

141   To examine the potential consequences of indoor populations of harmful alien ant species
142   naturalizing under warming scenarios, we obtained the impact score of each species in outdoor
143   environments from a recent impact assessment of alien ants globally (21), followed by summing
144   these scores across harmful species within each region. Thus, the cumulative impact scores of a
145   region reflect the potential impacts of all naturalized species. Scores for environmental and
146   socioeconomic impacts were calculated separately. Among the 137 regions with ≥ 1 harmful ant
147   population, the highest impact score in outdoor environments was observed in California and
148   Georgia (US state) (score=73; Figure S1e), while for socioeconomic impacts the highest was
149   observed in Texas (score=53; Figure S1f).

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The roles of climatic conditions in restricting alien ants indoors
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152   Using a generalized linear mixed model with a binomial error distribution, we assessed the
153   importance of temperature and water availability and seasonality in regulating the indoor status of
154   alien ants in different regions, while controlling for their introduction year based on their first
155   detection. We found that alien ants from warm environments with a low temperature seasonality
156   were more likely to be restricted indoors when introduced to relatively colder environments with a
157   higher temperature seasonality (Figure 1, Table S2). However, regardless of climatic conditions in
158   their native ranges, alien species had a high probability of establishing outdoors when introduced
159   to warm environments with a low temperature seasonality. We detected limited effects of water-
160   related climate variables as well as the associated vertical habitat strata and the introduction year
161   in determining the indoor statuses of alien species in non-native regions. These results were
162   robust to exclusions of potentially undersampled regions (i.e., regions with ≤ 2 indoor
163   populations), thus likely reflecting ecological processes rather than data biases across climatic
164   gradients (Table S3). The final model included only an interaction term between the temperature
165   regimes in a species' introduced range and the temperature regimes in its native range (R^2_m =
166   0.50; R^2_c = 0.94). We detected weak phylogenetic (Moran's I = 0.04) and spatial autocorrelations
167   (0.04) in the residuals of the final model.

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Predicted spread of indoor alien ants under climate change
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170   Projecting the final model to future climate change scenarios from TerraClimate (40), we
171   found that the average probability for 503 indoor alien populations to subsequently spread into
172   outdoor environments under the 2°C and 4°C warming scenario increased by 3.5% (range = 0–
173   25.0%) and 14.1% (0–67.4%), respectively. We recorded similar increases for the 298 indoor
174   harmful populations analyzed, with the average probability increased by 3.3% (0 – 25.0%) and
175   12.6% under the 2°C and 4°C (0–66.0%) warming scenario, respectively.

176   Under the 2°C warming scenario, the average gain in naturalized alien and harmful species
177   within regions through the spread of indoor populations was 2.1% (mean species gain = 0.1;
178   range = 0–1.5) and 3.3% (mean = 0.1; range = 0–0.6), respectively (Figure 2a-d). Nevertheless,
179   the increases relative to current naturalized alien and harmful species richness could be as high
180   as 66.9% and 38.1% respectively, indicating high variation among regions. The increases in alien
181   and harmful species richness were higher under the 4°C warming scenario, with the former
182   increasing by 8.2% (average = 0.5; range = 0–4.7) and the latter increasing by 12.7% (average =
183   0.3; range = 0–1.8) on average. Again, we observed high spatial variations in the relative
184   increases across regions, with the number as high as 259.0% and 128.5% for alien and harmful
185   species richness, respectively.

186

Predicted impacts by indoor alien ants under climate change

We found that 90 of the 137 regions having ≥ 1 indoor harmful population currently would have increased environmental impacts in outdoor environments under warming, while 68 regions would have increased socioeconomic impacts. Impacts on plants (42 regions), animals (40 regions) and enhanced competition (65 regions) would be the most prevalent environmental impacts associated with the naturalization of indoor harmful populations, while crop loss (61 regions), animal production (53 regions), and infrastructure (48 regions) would be the most prevalent socioeconomic impacts (Figure S2). The enhanced environmental and socioeconomic impacts would be strongly driven by the spread of indoor populations of *Linepithema humile* in 28 regions, even though this species did not have the highest number of indoor populations and the highest cumulative increase in naturalization probability across populations (Figure S3). Other notable species driving increased environmental and/or socioeconomic impacts under warming included *Paratrechina longicornis* (23 regions), *Pheidole megacephala* (6 regions), *Tetramorium bicarinatum* (19 regions), and *Tapinoma melanocephalum* (40 regions). Under 2°C and 4°C warming, the average increases in environmental impacts across regions were 2.3% (mean score increase = 0.3; range= 0-4.1) and 8.9% (mean = 1.3; range = 0-12.2), but maximum increases could reach 29.2% and 120.1%, respectively (Figure 2e-f). Socioeconomic impacts within regions would also be increased by 2.2% (mean = 0.2; range = 0-2.6) and 8.5% (mean = 0.8; range = 0-7.1) on average under 2°C and 4°C warming, but maximum increases could reach 62.7% and 177.7%, respectively (Figure 2g-h).

In all future climate scenarios, the projected gains in naturalized alien and harmful species, as well as the associated impacts, were largest in the Northern Hemisphere, particularly in the USA and European regions such as Italy, France, and Finland (Figure 2, Figure S4). We detected strong correlations between the two future climate scenarios in their projected gains in alien and harmful species richness, environmental impacts, and socioeconomic impacts (Kendall's tau > 0.82). Limiting warming to 2°C would reduce gain in naturalized alien and harmful ant species richness and the associated impacts in all regions, with the reduction being more prominent in European regions and the USA (Figure S3).

Countries' capacities to control the potential spread of indoor alien ants

Extracting country-level scores on response capacity to biological invasions from Early and colleagues (22), we examined whether the effects of climate change in facilitating the naturalization of alien and harmful species and the associated impacts were restricted to countries with high response capacity. We found that climate change effects on indoor alien ant populations were highly heterogeneous at the country level (Figure S5). The top 10 countries were associated with > 62.3% of climate change effects, while the top 20 were associated with > 82.6% (Table S4). We recorded minimal effects in countries that had a total response capacity score < 2.5. Less than 26.9% of effects would occur in countries with a comprehensive response capacity in all aspects (i.e., Total score = 5). Instead, most effects would be associated with countries that had a total score ranging from 3-4 (Figure 3).

Of the top 20 countries predicted to suffer the strongest effects from the naturalization of indoor populations with climate change, only five—namely, the USA, UK, Canada, Chile, and Austria—had full scores in response capacity. All highly threatened countries except Luxembourg recognized the threats of invasive species, and > 70 % had developed a comprehensive list of current or potential invasive species (Figure 4). We detected the greatest shortfall in managing biological invasions (e.g., policies, legislations, and resources that target problematic invasive species nationally), followed by monitoring (e.g., facilities to report biological invasions, disseminating resources for identifying invaders) among the highly threatened countries. Depending on warming scenarios, only 25– 30% of the 20 most threatened countries had "comprehensive" invasive species management, while 55 – 65% had established monitoring schemes, and 70 – 85% had existing research on invasive species. Considering only the top 10 countries did not change the conclusions (Figure 4, Table S5).

239
Discussion
241 We examined how climatic conditions restrict alien ant populations to indoor environments, and
242 how climate change would facilitate the spread of indoor alien populations to outdoor
243 environments (i.e., naturalization) and generate extra environmental and socioeconomic impacts.
244 We further evaluated whether these anticipated spreads would be concentrated in countries with
245 comprehensive response capacities to biological invasions. We observed that alien ant species
246 introduced to regions with low and seasonal temperatures had a higher probability of establishing
247 indoor populations if their native range had dissimilar climates. However, climatic similarities
248 between native and non-native regions largely did not influence the naturalization success of
249 alien ant species in warm environments with a low temperature seasonality. Our findings from a
250 global analysis of 323 alien ant species demonstrate the generalizing role of indoor environments
251 as unique microclimatic bridgeheads for alien ants to bypass macroclimatic filters posed by low
252 and seasonal temperatures. This expands on previous studies focused on individual regions and
253 species (11, 14). Additionally, our results suggest that the continuous warming of the global
254 climate will erode macroclimatic filters and facilitate the naturalization of indoor alien ant
255 populations, including species that cause negative impacts. Warming extent is crucial in
256 determining the increases in alien species and associated impacts, with all metrics increased by
257 2-3% and 8-9 under 2°C and 4°C warming, respectively. Moreover, we found that the
258 naturalization of indoor alien populations with climate warming is more likely to occur in regions
259 lacking comprehensive capacities to manage and monitor biological invasions. Altogether, these
260 findings highlight the role of indoor populations in exacerbating alien ant invasions globally under
261 climate change, which is unlikely to be contained by current invasive species management,
262 adding to the already high negative impacts generated by invading ants (21, 35).

263 We found partial support for the climate matching hypothesis (15), as increasing climatic
264 similarities between native range and invaded regions were important for outdoor establishments
265 of alien ants in cold environments with a high temperature seasonality only. In fact, our database
266 has few records of indoor alien populations in warm environments with a low temperature
267 seasonality, in contrast to their preponderance in cold environments with a high temperature
268 seasonality. On average, the critical maximum thermal limit for ants lies at 46°C, while the critical
269 minimum thermal limit lies at 5°C (41). Considering the spatial scales (i.e., ~ 4km) of our climatic
270 data, outdoor conditions in cold regions can frequently drop below 5°C in winter, while in warm
271 regions the temperature can rarely exceed 46°C (40). This indicates that climatic conditions in
272 cold regions can be more lethal than warm regions for alien ants generally. Additionally,
273 relationships between climatic conditions in the native ranges of ant species and their critical
274 maximum thermal limits are less clear compared with their critical minimum thermal limits (41).
275 These could explain why we found support for the climate matching hypothesis in cold regions
276 only. Nevertheless, heat stress in warm regions can still cause substantial lethal and sublethal
277 effects on ants, such as increasing predation risks or reducing colony size (42, 43). Unlike lethal
278 effects, sublethal effects might not act to restrict alien ant species to indoor environments, but
279 only increase their associations with such environments. These sublethal effects would not have
280 been detected by the binary classification of indoor status in our analysis.

281 Since indoor environments help alien species escape from cold stress, warmer buildings
282 can be expected to be more important in driving invasion. Microclimatic conditions in indoor
283 environments can be affected by building designs, uses, and human behaviors, including wall
284 thickness, the frequency and consistency of temperature controllers uses, and their effectiveness
285 (44). Apart from having a suitable microclimate, indoor environments with high food and nesting
286 site availability can particularly favor ant invasions. Residential buildings and warehouses can
287 have high availability of anthropogenic food favored by generalist ants, a condition often observed
288 in introduced species, such as foods with high sugar and lipid contents, while the presence of
289 cracks and holes inside buildings provides nesting opportunities (45). Alternatively, indoor
290 environments used for cultivation can contain plants and sap-feeding hemipterans, which provide
291 extrafloral nectaries and honeydew to ants, respectively (39, 46). The introduction of insects used

292   as biological control agents in these indoor environments can also increase prey availability for
293   ants (39). Another unique aspect of indoor environments for cultivation is the increased presence
294   of trees relative to other indoor environments, providing nesting sites to arboreal ants. Indoor
295   environments can also support fewer invertebrate and vertebrate predators of ants, especially
296   those with large body sizes, leading to releases from natural enemies (47). These unique features
297   could make indoor environments easily invaded, especially if alien ants are able to naturalize,
298   which would facilitate their dispersal and ultimately increase establishments and negative impacts
299   in other indoor environments, a phenomenon that has been observed in other greenhouse pests
300   such as moths (48).

301   As climatic conditions in indoor and outdoor environments can be largely decoupled, indoor
302   records should be excluded from distributional data if studies are primarily interested in assessing
303   the risks of outdoor environments to biological invasions or how species expand their niche
304   through invasions. Popular sources of distributional data, such as GBIF, can contain indoor
305   records, and previous studies did not always remove them before analyses (49–52). When indoor
306   records are very prevalent in the dataset, or when they act as outliers (53, 54), climatic niche and
307   species' abilities to establish under novel climate can be overestimated, subsequently leading to
308   erroneous risk assessments on sites susceptible to invasions and species likely to become
309   invasive (55). Including indoor records can also influence conclusions of processes driving
310   invasion patterns, such as reducing the importance of climatic variables due to the lack of
311   macroclimatic filters in indoor environments, and increasing the importance of propagule pressure
312   (4), potentially misleading management practices.

313   Our findings reveal a lack of comprehensive capacities to control or prevent future biological
314   invasions among countries that are highly susceptible to the spread of indoor alien populations to
315   outdoor environments. These shortfalls are mainly related to the management and monitoring of
316   biological invasions, indicative of a lack of awareness, resources, personnel, and information
317   (22). Such countries could have limited implementations of measures controlling or eradicating
318   indoor alien populations, especially as these measures are often voluntary (56). Additionally, a
319   country's limited response capacity can exacerbate the difficulties it faces in incorporating the
320   effects of climate change into invasive species management due to overwhelming demands from
321   current invasions (57). The lack of planning for climate change can impede early detection and
322   rapid response in indoor and outdoor environments in the future, which are crucial to minimizing
323   the negative impacts of biological invasions (57, 58).

324   In this study, we aimed to examine the importance of climatic drivers in restricting alien ant
325   species to indoor environments, at least for species that are likely to escape (i.e., excluding
326   species that are pets and restricted within terrariums (59)). We did not seek to undertake a
327   comprehensive assessment of the effects of climatic drivers on biological invasions, as this would
328   require information on failed establishment events following introductions, for which data are
329   presently unavailable. As our results do not capture the full effects of climatic drivers on biological
330   invasions, our climate change projections solely relate to the effects of climate change in
331   facilitating the spread of indoor populations to outdoor environments, and should not be
332   interpreted as absolute forecasts of future alien species richness in the outdoor environments of
333   different regions. An accurate forecast of naturalized alien species richness and their associated
334   impacts outdoors would also need to consider other invasion pathways, such as propagules from
335   trade (including but not limited to pet trades) and spread from nearby countries (11, 59). Still, our
336   results evidence how warming can systematically exacerbate the impacts of a key but poorly
337   understood invasion pathway—populations of alien species residing indoors (11).

338   Overall, our results evidence indoor environments as important microclimatic bridgeheads
339   for the invasions of alien ants to regions with low and seasonal temperatures, especially for
340   species that originate from regions with dissimilar temperature regimes. The continuation of
341   climate warming is expected to facilitate the naturalization of indoor-confined alien ant species
342   and cause extra socioeconomic and environmental impacts, with the average increases across
343   regions tripled under the 4°C warming compared with the 2°C warming scenario. Although our

344 analyses are restricted to ants, these findings should broadly apply to taxa that display high alien
345 species richness indoors, such as various terrestrial invertebrates (6, 8, 10), plants (7), and fungi
346 (60). These taxa are known to contain some of the worst invaders, therefore the naturalization of
347 their indoor populations should also lead to extra environmental and socioeconomic impacts
348 under climate change (20, 61). Managing the extent of warming could be key in limiting impacts
349 contributed by the spread of indoor alien populations to outdoor environments. Failure to limiting
350 warming would require strengthening response capacities, especially in the management and
351 monitoring of alien species (22), to minimize impacts of these anticipated invasions.

352

353 **Materials and Methods**

354

355 **Data sources**
356 Our study involved four databases, and their brief descriptions are provided here. Full
357 descriptions are provided in Supporting Information Text S1.

358 For ant occurrences, we used The Global Ant Biodiversity Informatics (GABI), which
359 contained nearly 2.5 million ant occurrence records extracted from the literature (~10,500 studies)
360 and ant specimen database (25). The database indicated the native and non-native range of each
361 species. Classifications of alien ant populations followed (19), with "Indoor" defined as
362 populations restricted indoors, while "Naturalized" defined as populations established outdoors.
363 Records known only from quarantine and thus indicative of transportation but not of
364 establishment were not included. Ultimately, for species that had at least ≥1 non-native
365 occurrence worldwide, the database identified 5,220 alien populations (i.e., unique combinations
366 of species and region) and 12,354 native populations.

367 We obtained impact scores from a recent global risk assessment of alien ants (19). The
368 database contained 1,162 impact records of 34 species from 642 studies. 16 species were also
369 listed in the Global Invasive Species Database (62). We extracted impact scores of each ant
370 species based on the Generic Impact Score System (GISS), which was based on six categories
371 of environmental (e.g., Competition with animals) and socioeconomic (e.g., Infrastructure
372 damage, crop loss) impacts.

373 Current and future climatic conditions were obtained from TerraClimate, a database of ~4
374 km resolution (40). The minimum temperature of the coldest month, the maximum temperature of
375 the warmest month, total precipitation, and soil moisture in both the driest and wettest months
376 were considered. Seasonality of temperature, precipitation, and soil moisture were also
377 considered. We used the 2°C and 4°C warming scenarios for subsequent model projections. As
378 climatic variables are highly intercorrelated (R > 0.7 or < -0.7), we used PCA separately for
379 temperature and water availability variables and ultimately extracted the two PCA1 scores for
380 each grid globally.

381 Response capacity to biological invasions was obtained from (22). The database scored
382 response capacity in 2015 based on countries' reports to the Convention of Biological Diversity
383 (https://www.cbd.int/reports). The scores of five categories were extracted, namely if 1) countries
384 recognized invasion threats, 2) a list of invasive species was available, 3) management practices
385 controlling invasive species existed, 4) there were research and international collaborative
386 programs to prevent or mitigate the impacts of invasive species, and 5) invasive species was
387 monitored. The scores of each category were either 0 ("No") / 1 ("Yes") or 0 ("None") / 0.5
388 ("Limited") / 1 ("Comprehensive").

389

Modelling indoor status

We first extracted PCA1 scores from each grid within the native distribution of each species and averaged them to represent the climatic conditions in their native distribution. We also obtained average PCA1 scores for each region in the introduced range. Finally, we designated the timing of the earliest record of an alien species within a region as its introduction year, which would be used to control propagule pressure (1). We dropped populations that had no dated records (as we included the earliest date of detection as a covariate in the model to proxy propagule pressure, see below), as well as 14 species with no native distribution data available. These reduced the number of alien populations for subsequent analyses from 5,220 to 4,819.

As the response variable—the indoor status of each alien species in each region—was binary, we used generalized linear mixed models with binomial error distributions to regress indoor status against the predictor variables. The model included records of all species from all regions, and was built using the R package *glmmTMB* (63). The predictors included were the PCA1 of both the temperature and water variables in the introduced and native range. In addition, we specified two two-way interaction terms in the model: temperature PCA1 in the native distribution and the introduced region, and water PCA1 in the native distribution and the introduced region. Inclusions of interaction terms assess how climatic conditions in introduced regions filter species based on their native distributions (64).

We additionally included covariates to isolate the effects of climatic drivers further. First, we added the introduction year as a covariate to act as a proxy for propagule pressure (1). Introduction year was log-transformed to reduce skewness. Second, we used data on the vertical habitat strata occupied by each alien ant species from Wong and colleagues (19), which indicated whether a species was associated with the litter-and-soil, ground-surface, and/or arboreal strata. In our data, 43 (13%) species occupied more than one stratum, with 21 occupying the ground surface and the arboreal strata, 16 occupying the ground surface and the litter-and-soil strata, and 6 occupying all three strata. We created three new categories for these species, leading to six categories of vertical habitat strata ("litter-and-soil", "ground", "arboreal", "ground and litter-and-soil", "ground and arboreal", "all") in total.

For the random effect structure, we first added polygon and species identity as random intercepts. We also added climatic predictors as random slopes in the model, allowing their effects to vary across polygons or species, which helped minimize type-I and type-II errors (65). Our random effect specifications followed recommendations from simulation studies on trait-environment interactions (64). Introduction year and strata, however, were not added as random slopes to facilitate model convergence, as they were not the primary interest of this study (66). In *glmmTMB*, the full model was specified as

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)

We dropped any insignificant interaction terms and reassessed the significance of the main effects (67). If these main effects were still insignificant, we removed them from the final model, which would be used for climate change projections. To ensure our results were robust to spatial and phylogenetic autocorrelation, we quantified Moran's I in the residuals of the final model. For spatial autocorrelation, the distances between polygons were calculated based on their centroid. For phylogenetic autocorrelation, we obtained phylogenetic distance from the genus-level phylogenetic tree for ants (68). After converting the tree to ultrametric using UPGMA (Cophenetic correlation coefficient between the unconverted and converted tree = 0.96), eight missing genera (11 % of total genera) were placed as basal polytomies of their sister genus in the tree (Table S6). Autocorrelation assessments were conducted using the R package *DHARMa* (69).

Data biases could affect our results by confounding the signals of climatic variables. For instance, indoor environments in the tropics could be more undersampled compared with

440 temperate regions. These methodological biases could co-vary with climatic gradients, which
441 would lead to a pattern that most alien ants are able to naturalize under tropical climate.
442 Unfortunately, quantifying the extent of undersampling in each region would be impossible. Thus,
443 we used the number of indoor populations as an indicator of undersampling, and assumed
444 regions with 1) no indoor alien populations, 2) ≤ 1 indoor population, and 3) ≤ 2 indoor
445 populations as "undersampled". We repeated our analyses without these regions to ensure our
446 results reflect climatic effects but not sampling biases across climatic gradients.

447

448 **Climate change projections**
449   Future PCA1 scores were obtained for the introduced range, but not in the native
450 distribution, as we are primarily interested in climate change effects on driving future invasions.
451 We projected the final model above using current and future climate conditions for each
452 introduced polygon in *glmmTMB* (63). In the projections, we included all established populations
453 regardless of their indoor status and obtained naturalization probability for each population. We
454 calculated the effects of climate change on each population as differences in their naturalization
455 probability between future and current climates. Theoretically, indoor populations could have an
456 increased probability of naturalization, and naturalized populations could have a decreased
457 probability, suggesting they would be more restricted indoors under climate change. However,
458 our projections showed that naturalization probability was at most reduced by 0.1% and 0.5%
459 across all naturalized populations under 2°C and 4°C warming scenario (n=4,316). Thus, in
460 subsequent analyses, we only considered changes in the naturalization probability for indoor
461 alien populations (n=503).

462   We calculated the expected gain in naturalized alien species by summing the differences in
463 naturalization probability between current and future scenarios across all indoor alien populations
464 in each region. We also calculated the gain in "harmful" species in each region by restricting the
465 analyses to 34 ant species with negative environmental and/or socioeconomic impact records in
466 their non-native range (21) (Table S1).

467   To examine how the naturalization of indoor harmful populations under climate change can
468 generate additional environmental and socioeconomic impacts in outdoor environments, we
469 calculated gains in cumulative impact scores of each region across all indoor harmful populations
470 between current and future climate scenarios. Specifically, the differences in cumulative impact
471 score in each region between future and current climate were calculated as

472
$$\sum_{i=1}^{n} \sum_{j=1}^{6} (P_{i,Future} - P_{i,Current}) \times Score_{i,j}$$

473 where n was the number of harmful species with indoor populations, $P_{i,Future}$ and $P_{i,Current}$ were
474 the naturalization probability for species *i* under future and current climate, and $Score_{i,j}$ was the
475 impact score of species *i* in category *j*. Environmental and socioeconomic impacts had six
476 categories and were calculated separately, thus the maximum number of j was 6. When there
477 were multiple scores available for the same impact category, we used the maximum score for
478 each species, a common approach in invasive species risk assessments (21). While species
479 might never reach the observed "maximum" impacts in some regions, a higher cumulative impact
480 score still indicates high potential impacts by alien ants within regions, implying increased risks to
481 management (70, 71). We assumed that the species had no impact on the categories if no
482 records were available.

483   To quantify the future increases of impacts relative to current impacts in outdoor
484 environments, we calculated the cumulative impact scores under current climate conditions by
485 summing impact scores across each naturalized harmful species in each region, with their
486 naturalization probability set as one. The impacts of all indoor populations in outdoor

487 environments were set to zero. We also calculated the sum of gains in the cumulative impact
488 score of each category across all regions under climate change to better understand the primary
489 mechanisms driving increased socioeconomic and environmental impacts. Additionally, for each
490 species, the cumulative changes in environmental and socioeconomic impact scores across all
491 indoor populations globally were calculated separately to uncover which would be most
492 responsible for increasing future impacts.

493

494 **Response capacity analyses**
495 As the response capacity data was at the country levels (Figure S6), we upscaled the
496 regional impacts to minimize spatial mismatches, such as all states in the USA (except the
497 minority outlying islands) being aggregated. This also prevented larger countries from biasing the
498 analyses since they were associated with more regions than smaller countries. Briefly, we used
499 the gain in naturalization probability, environmental impacts, and socioeconomic impacts in the
500 worst-affected region to represent each country (see Text S2 for details). Since we were primarily
501 interested in the threats posed by indoor populations, we only included countries (n = 54) with ≥ 1
502 indoor population and response capacity data available for the analyses.

503 To assess if the facilitated spread of indoor alien populations to outdoor environments by
504 climate change would be restricted to countries with a comprehensive response capacity, we
505 obtained each country's total response capacity by summing scores across the five categories.
506 We then calculated the sum of gain in the naturalization probability of alien and harmful species,
507 environmental impacts, and socioeconomic impacts under climate change for each level of the
508 total score. To identify the weakest aspects of response capacity, we also assessed the
509 proportion of highly threatened countries with existing or comprehensive policies in different
510 aspects. To ensure our results were not sensitive to arbitrary thresholds, we assessed the
511 response capacity of the top 10 and 20 countries with the highest projected gains in each metric
512 and scenario.

513
514 **Acknowledgments**
515

520

521 **References**

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Figures and Tables
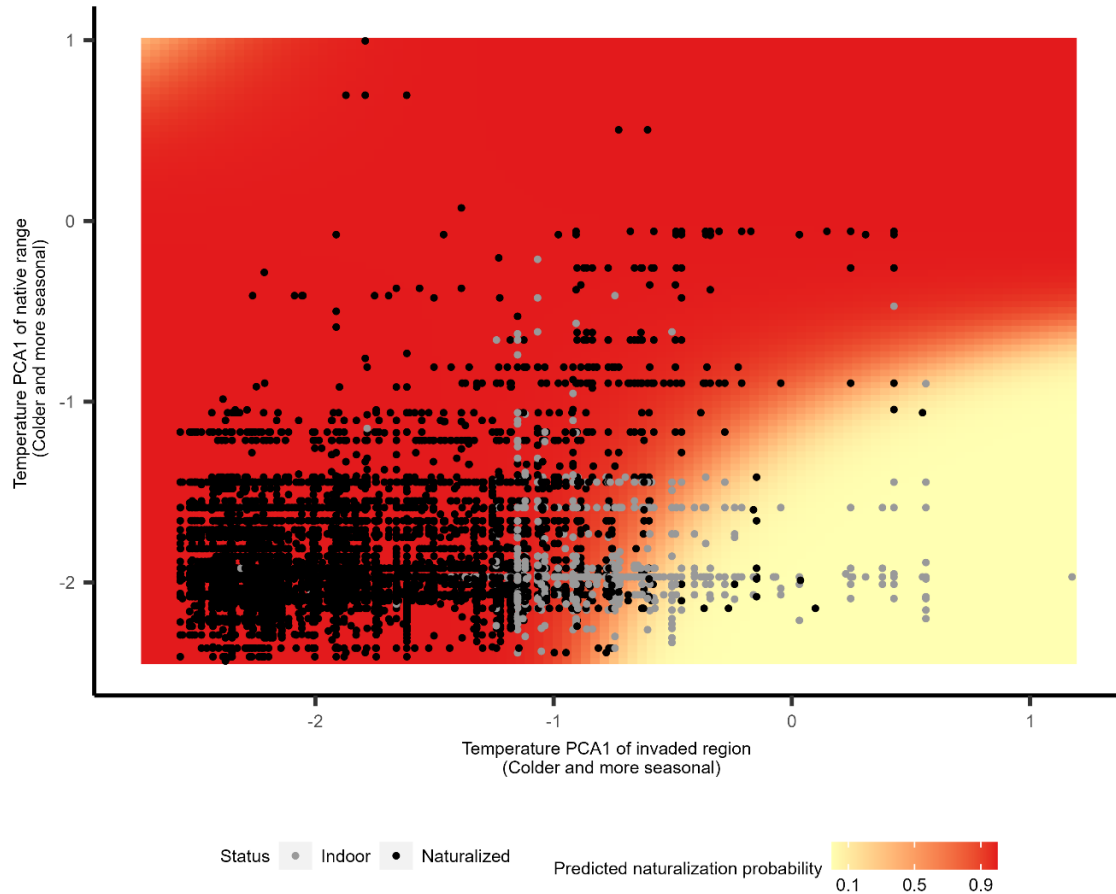
689   **Figure 1.** Cold-distributed species have a higher probability of establishing outdoors compared
690   with warm-distributed species when invading cold regions. In warm regions, however, all
691   incoming alien species are expected to establish outdoors regardless of the climate of their native
692   range. Extremely cold-distributed species could have a lower probability of outdoor establishment
693   in very warm regions (i.e., upper left corner), although these apply to hypothetical scenarios only.
694   Each data point represents an alien species established in an introduced region, with grey and
695   black colours representing establishments in indoor and outdoor environments, respectively.
696   Increasing PCA1 scores along both axes indicate colder and more seasonal temperature
697   regimes, with Y-axis and X-axis indicating the climate in the native range of each species, and the
698   climate in the invaded region of each population, respectively. Predicted naturalization
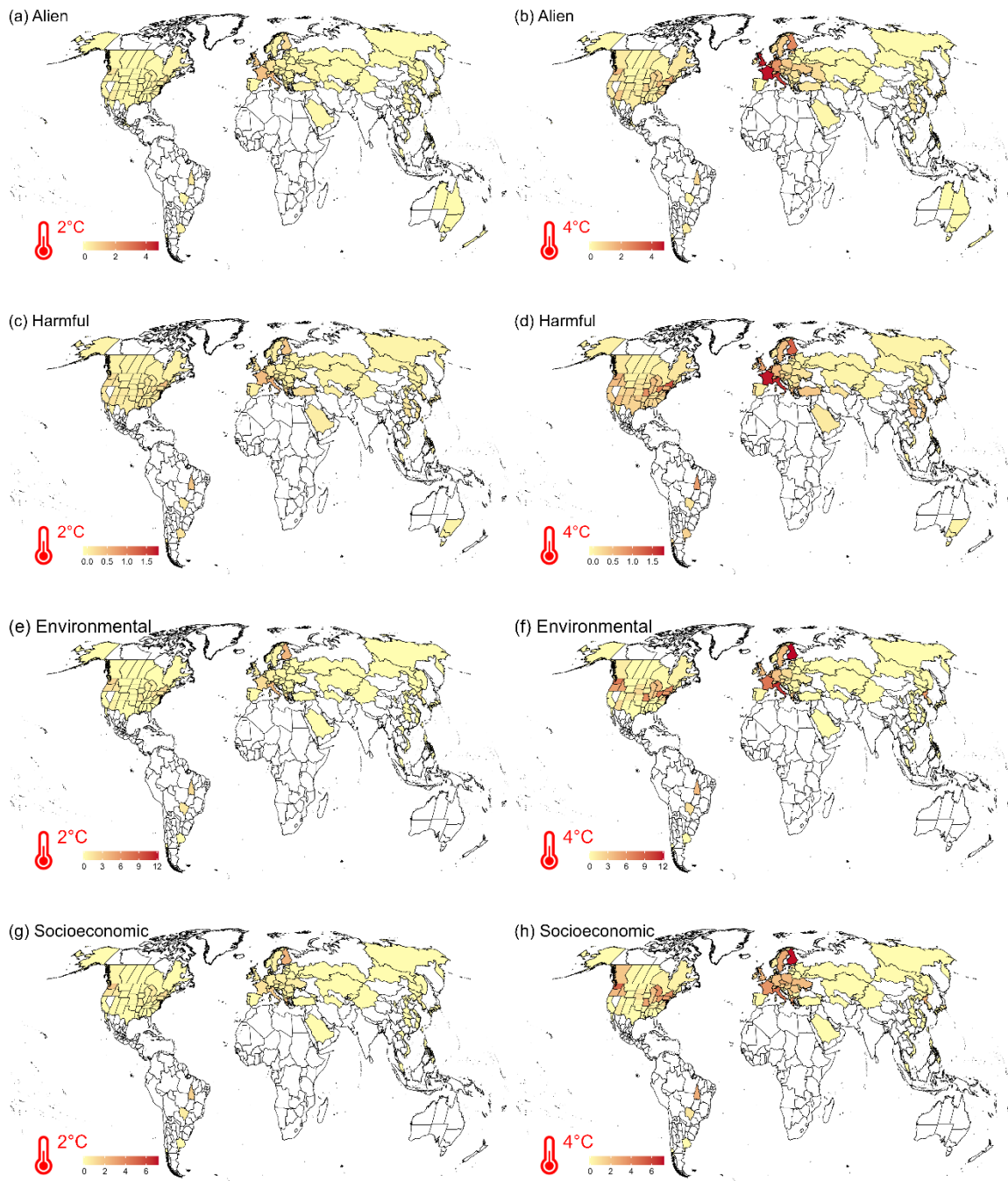699   probabilities are based on the fixed (but not random) effects of the full model.

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Figure 2. Projected gains in alien 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 alien (a,b) and harmful populations (c-h). Projections are based on the random and fixed effects of the final model.
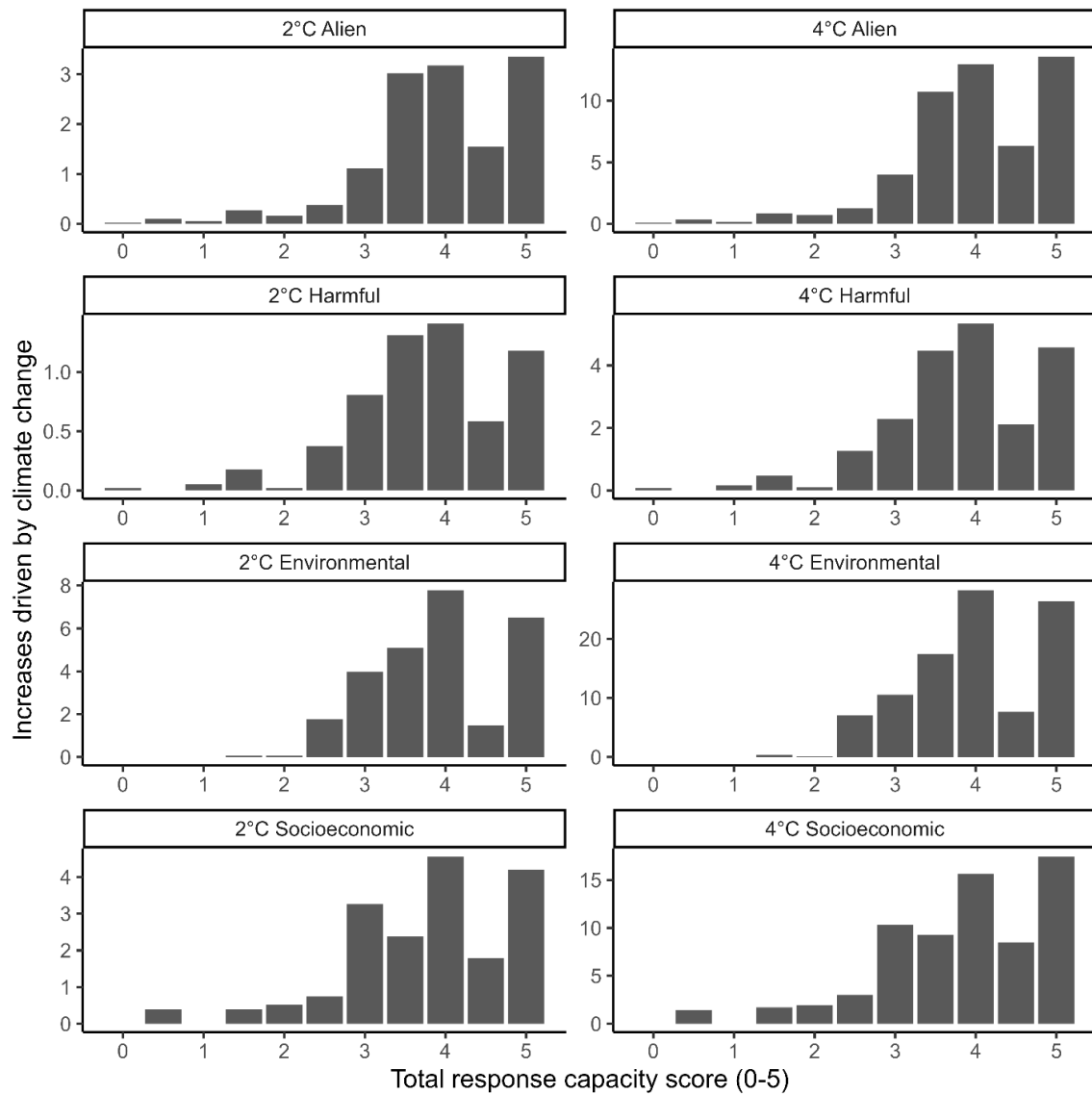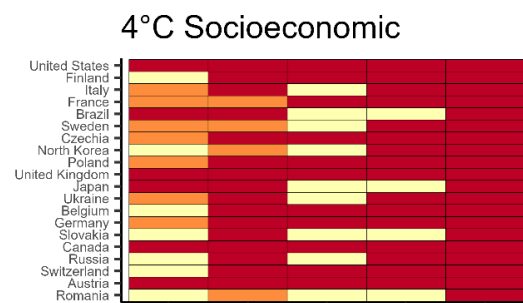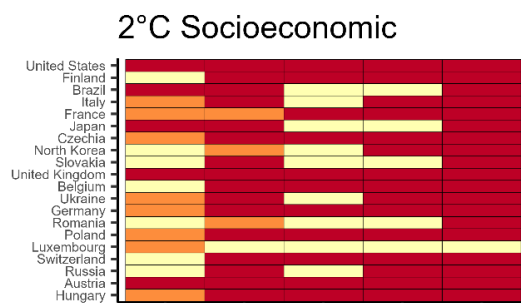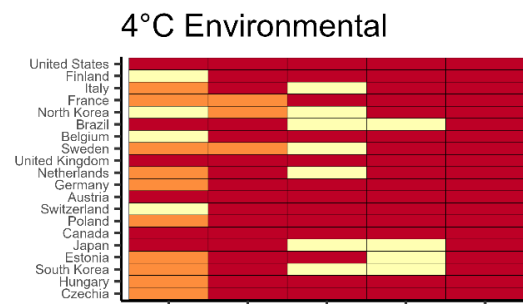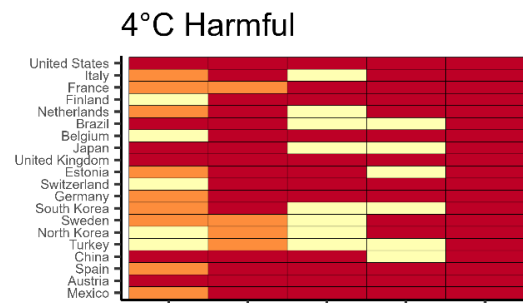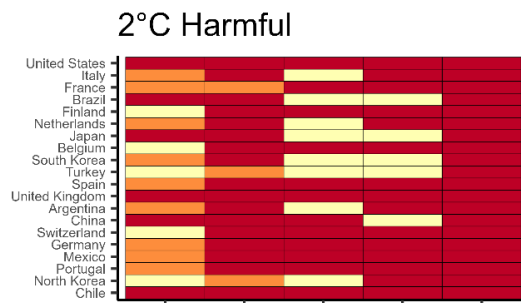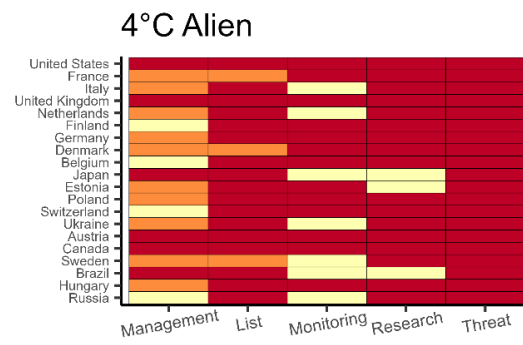
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Figure 3. The impacts of climate change in facilitating the spread of indoor alien population to outdoor environments across different levels of total response capacity. Climate change impacts are calculated as the sum of gain in naturalization probability, environmental impacts, and socioeconomic impacts across countries with the same total response capacity scores. Thus, a higher value along Y-axis indicates more severe impacts of climate change. A higher score in response capacity (i.e., X-axis) indicates more comprehensive policies on biological invasions.

2°C Alien
4°C Alien
2°C Harmful
4°C Harmful
2°C Environmental
4°C Environmental
2°C Socioeconomic
4°C Socioeconomic

Score: 0 / 0.5 / 1

720
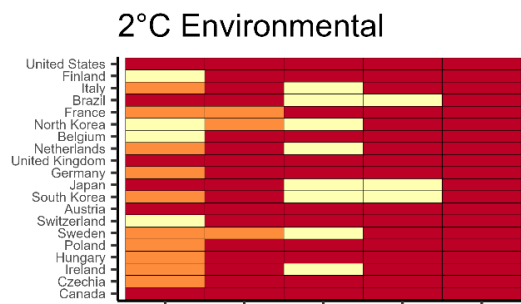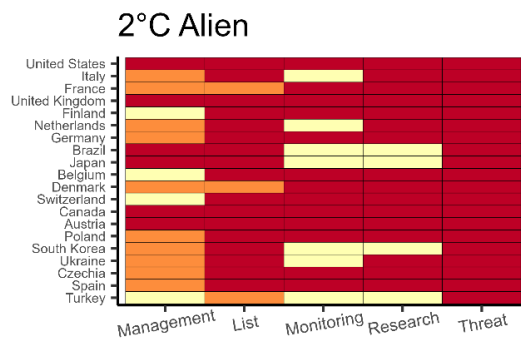
721   **Figure 4.** Scores of response capacity in top-20 countries with the highest projected gains in
722   invasive species richness in outdoor environments under two warming scenarios. Countries at the
723   top of the y-axes are projected to experience the highest gains in the species richness of invasive
724   ant species due to the anticipated spread of indoor alien populations to outdoor environments
725   under climate warming. A country with comprehensive policy in certain aspects would be scored
726   as 1.
727
728

PNAS

Supporting Information for

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

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This PDF file includes:

       Supporting text S1 to S2

       Figures S1 to S6

       Tables S1 to S6

Supporting Information Text S1 – Detailed descriptions of each database

730 **Alien ant records**
731 The Global Ant Biodiversity Informatics (GABI) extracted nearly two million ant occurrence
732 records from the literature (10,500 publications) and specimen databases, such as AntWeb,
733 museum collections, and personal collections. GABI records were compiled and checked by ant
734 experts to maximize reliability (1). To maximize the geographic resolution of the distribution data
735 and as many records (especially older records) were not georeferenced, a system of 546
736 polygons was used for analyses, where an occurrence record could correspond to either a
737 country or a lower administrative unit for large countries such as China and the United States.
738 Some records reflected natural rather than political boundaries, such as island systems, including
739 the Lesser Antilles (see details in (1)). The database used species' mentions in the literature, their
740 number of records within a zoogeographical realm or region, and the locality and habitat of the
741 collection to determine the native and non-native range of each species. Subspecies were
742 considered separately in the database, but hereby we collectively term them as species.

743 We defined the indoor status of each non-native record following terminologies from the
744 database (2). "Indoor" was defined as populations only occurring in indoor environments such as
745 greenhouses and buildings, while "Naturalized" was defined as populations established in outdoor
746 environments. Any records of alien ants merely intercepted at borders or which reflected an
747 uncertain introduction and indoor status were excluded from the analysis. Where there were
748 multiple occurrence records for the same alien species within a region, we classified that
749 population (i.e., unique combinations of regions and species) as "indoor" only if all records
750 unanimously suggested that the species was restricted to indoor environments in the region, and
751 classified the species as "naturalized" if the different records had conflicting statuses.

752 The year of each record was either their publication year, or the time that the record was
753 made according to the literature. This information would be used as a proxy for the year of
754 introduction in each region. For example, as *Linepithema humile* had eight dated records in the
755 UK between 1915–2016, with seven as "indoor" and one as "naturalized", we considered this
756 species to be "naturalized" in the UK and introduced in 1915.

757 Note that our dataset did not address alien ants from pet trade, which would also be
758 considered as indoor records by definitions. However, these pets were often contained within
759 terrariums, thus they are unlikely to escape and establish outdoors, even if outdoor conditions are
760 suitable for them. This would make them unsuitable for testing our hypotheses on the role of
761 climatic conditions in restricting alien ant indoors.

762

763 **Environmental and socioeconomic impacts of alien ants**

764 Previous studies have assigned impact scores for each alien species and obtained the sum of
765 these scores for each region to assess the potential impacts of biological invasions and prioritize
766 regions for management (e.g. (3, 4)). We obtained the scores of environmental and
767 socioeconomic impacts by alien ants from (5) to understand the potential consequences of indoor
768 alien ant populations spreading into outdoor environments. We used the scores of each alien ant
769 species in the Generic Impact Score System (GISS), a methodology considering the
770 environmental and socioeconomic impacts of alien species. We chose to use GISS instead of
771 other methodologies because they provided finer classifications of different impacts, and the
772 scores were based on 1,162 impact records from 642 studies. Environmental impacts contained
773 six categories: 1) plants or vegetation, such as alien ants affecting other ant species and
774 ultimately seed dispersal; 2) animals through predation, parasitism or intoxication; 3) competition
775 with other species; 4) ecosystem impacts, such as driving invasion meltdown; 5) disease
776 transmission; 6) hybridization. Socioeconomic impacts also contained six categories: 1) Crop

777 production; 2) Animal production; 3) Forestry production; 4) Human infrastructure and
778 administration, such as electrical damage and costs of managing invaded areas; 5) Human health
779 6) Social life, such as abandoning playgrounds due to ant infestation. The score of each category
780 ranged from zero (i.e., no impact) to five (i.e., severe impacts), thus theoretically a species can
781 have 60 points in total, although the highest score was 35 only when considering the maximum
782 scores of each category (5).

783   We excluded all low-confidence impact records. For human health impacts, we further
784 removed records that are unlikely to occur within outdoor environments, as our studies are
785 interested in the potential consequences of naturalization under climate change. Specifically, for
786 health impacts, we only considered records of ant attacks, even if these attack records were
787 conducted in indoor environments, as ants could attack people outdoors (6). We excluded scores
788 based on ants carrying pathogens, which is a health concern in indoor environments such as food
789 storage facilities due to the potential of food poisoning, but is a lesser concern in outdoor
790 environments. Additionally, ants are likely to acquire these pathogens when they forage in
791 contaminated areas such as hospitals, thus naturalized populations do not necessarily carry the
792 same pathogens (7). Scores based on ant occurrences within indoor environments only were not
793 considered, because these studies did not provide any evidence of their direct or indirect health
794 impacts, even though ant species were perceived as "nuisance" or "hygiene issues" within indoor
795 environments. Thus, seven "harmful" species had no negative impacts in outdoor environments
796 (e.g., *Monomorium pharaonis*).

797

Current and future climatic conditions of each region

799 As the dataset included a variety of soil-dwelling, surface-dwelling and arboreal ant species (2),
800 we characterized the climatic conditions of each polygon using the monthly minimum and
801 maximum air temperature, total precipitation, and soil moisture from the open-access database
802 TerraClimate, which has a ~4 km spatial resolution for current and future climate scenarios
803 (Abatzoglou et al., 2018). We characterized each grid using the minimum temperature of the
804 coldest month, maximum temperature of the warmest month, total precipitation and soil moisture
805 in both the driest and wettest month. Additionally, we calculated the standard deviation across
806 months for temperature, soil moisture and precipitation separately as a measure of seasonality.
807 For temperature, we calculated the average across the minimum and maximum temperatures in
808 each month, and obtained the standard deviation across all months as a measure of temperature
809 seasonality. We also extracted the minimum and maximum soil temperatures of the coldest and
810 warmest months at 0-5 cm and 5-15 cm deep from SoilTemp (8), but these data were not
811 included in subsequent analyses because forecasts for the impacts of climate change on soil
812 temperatures were unavailable. However, the omission of soil temperature is unlikely to affect our
813 results since they were highly correlated with air temperature under current climatic conditions
814 (Pearson's r > 0.91). We included the 2°C and 4°C warming scenarios, with the former
815 representing the upper limit of global warming target indicated in the Paris Agreement, and the
816 latter representing a "business-as-usual" outcome.

817   We first conducted a collinearity check on each climatic variable across the globe and found
818 high intercorrelations (R > 0.7 or < -0.7). Therefore, we conducted PCAs separately for
819 temperature and water variables based on current climatic conditions after standardization and
820 extracted PCA1 scores for both, as they explained 76% and 62% of variations, respectively. We
821 did not retain other PCA axes as their explanatory power was not higher than random, based on
822 a significance test in R-package *BiodiversityR* (8). Increasing PCA1 scores for all temperature
823 variables indicated cooler and more seasonal environments, while for water variables, they
824 indicated wetter and more seasonal environments. We then reprojected the two PCA models
825 using future climatic conditions to obtain future PCA1 scores of each grid.

826

Response capacity

To quantify response capacity to biological invasions, we used the database from (9), which scored countries' abilities to address invasive species threats in 2015 based on countries' reports to the Convention of Biological Diversity (https://www.cbd.int/reports). Dependent territories (e.g., overseas territories of France and UK, US minor outlying islands) were considered as separate units, and no scores were available for these regions.

The response capacity scores have been used to assess general response capacities to a variety of invasive taxa (e.g., (10)). Here, the scores were used as a proxy of response capacity to ant invasions, even though the scores were based on all taxa and not specific to ants. The database provided scores on six aspects of invasive species management, including whether 1) invasive species were recognized as threats to the economy and biodiversity of the country, 2) a national list of current and potentially problematic invasive species had been made, 3) there were management practices to regulate impacts of invasive species 4) there were measures to manage potential introductions of invasive species 5) there were international collaborations or research on controlling invasive species and 6) invasive species were monitored for potential expansion and emergence, including monitoring programs and awareness-raising campaigns. Since we were interested in the effects of alien ant populations which had already been established, we did not consider if there were measures to manage introduction (factor 4). Generally, these factors were either scored using two ("No" [0] / "Yes" [1]) or three categories ("None" [0] / "Limited" [0.5] / "Comprehensive" [1]). Note that the scores were comparative, and even countries with the highest scores could have insufficient capacity to manage biological invasions (Early et al., 2016). Nevertheless, the scores still captured capacity differences across countries and could be used to assess if any effects of climate change on the spread of indoor alien ant populations to outdoor environments would be limited to relatively well-managed countries. Additionally, the scores would help identify the weakest aspects of invasive species management in highly threatened countries.

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886

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

887

888 We used the maximum projected gain in outdoor establishment probability, environmental
889 impacts, and socioeconomic impacts under climate change to represent each species with ≥ 1
890 indoor population within a country. For example, *Monomorium floricola* had three indoor
891 populations in the US, and we used the population in the District of Columbia for country-level
892 analyses, as it had the highest projected gain under climate change. We then summed the gain in
893 outdoor establishment probability, environmental impacts, and socioeconomic impacts across
894 species within each country to represent climate change effects. These metrics reflect how
895 climate change will drive indoor populations to spread into outdoor environments, expanding their
896 distribution within countries and increasing impacts. Note that gains in outdoor establishment
897 probability does not reflect gains in alien or invasive species richness at the country level
898 because some indoor populations have naturalized in other regions within the same country.

899   In some regions where one country has a disproportionately larger area than others, we
900 used the largest country to represent the region. Examples include the region "continental Italy"
901 represented by Italy despite the presence of Vatican and San Mariano, and "Malaysia and
902 Singapore" represented by Malaysia. There were regions associated with multiple countries with
903 more comparable size (e.g. "Borneo", "Israel and Palestine", "Sudan", "Cyprus"), but they did not
904 contain any indoor populations and therefore would not affect the country-level analyses.
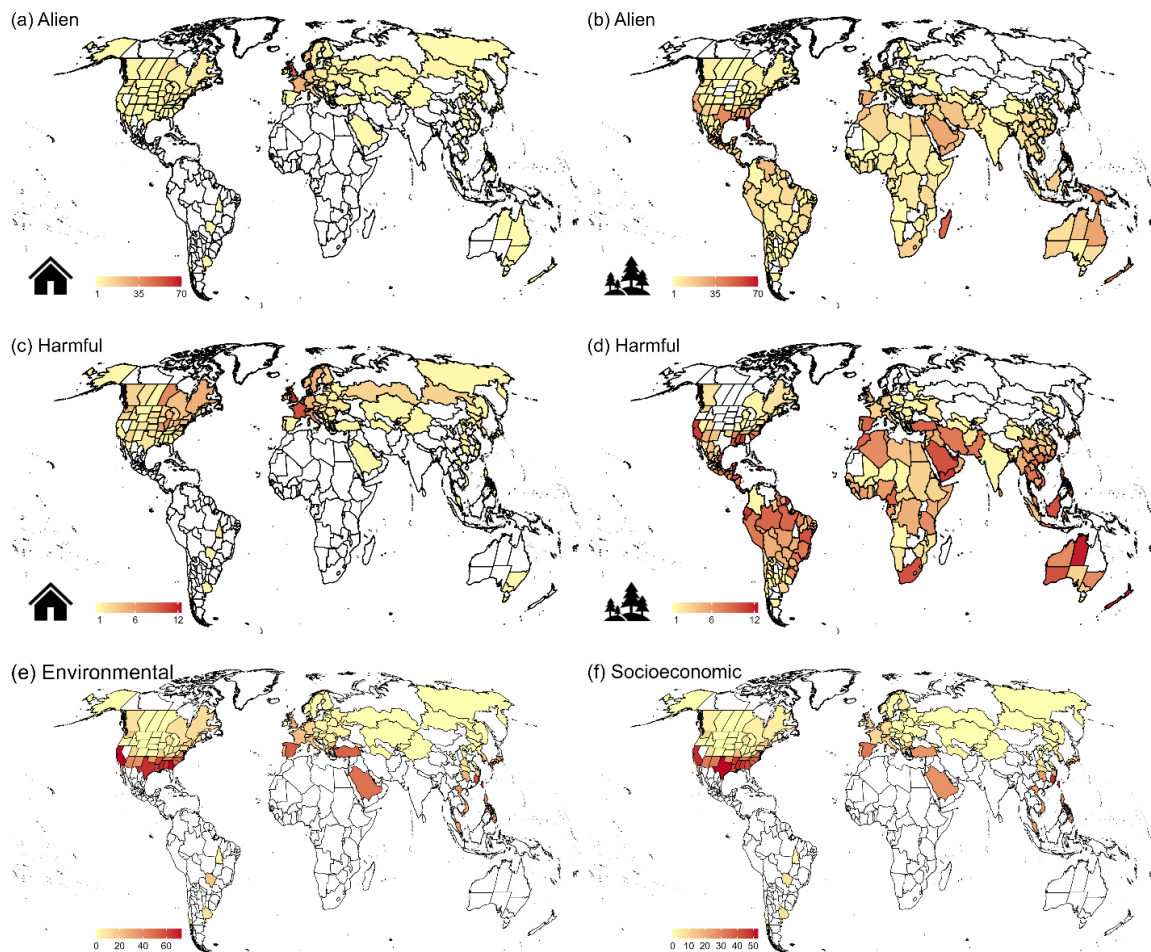
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908
Fig. S1. Global distribution of alien (a,b) and harmful (c,d) ant species richness in indoor (a,c) and outdoor (b,d) environments, as well as environmental (e) and socioeconomic impacts (f) in outdoor environments. In panel a-d, regions in white lack records for alien (a,b) and harmful (c,d) ant species established in indoor and outdoor environments. In panel e-f, regions in white lack harmful species within indoor environments. Higher values in panel e and f indicate higher impacts of harmful ants in outdoor environments.
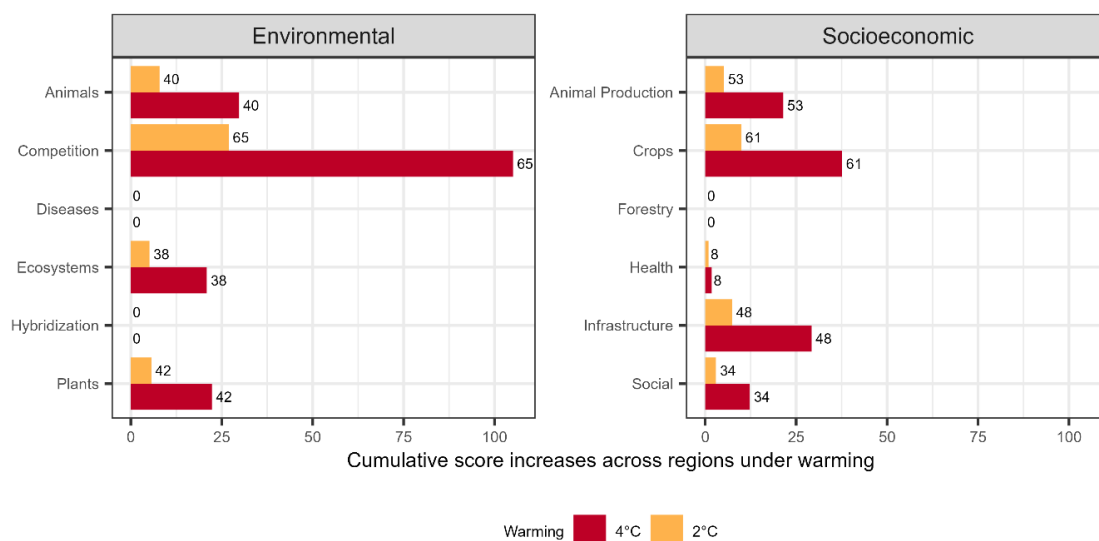
915
916

Fig. S2. 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.
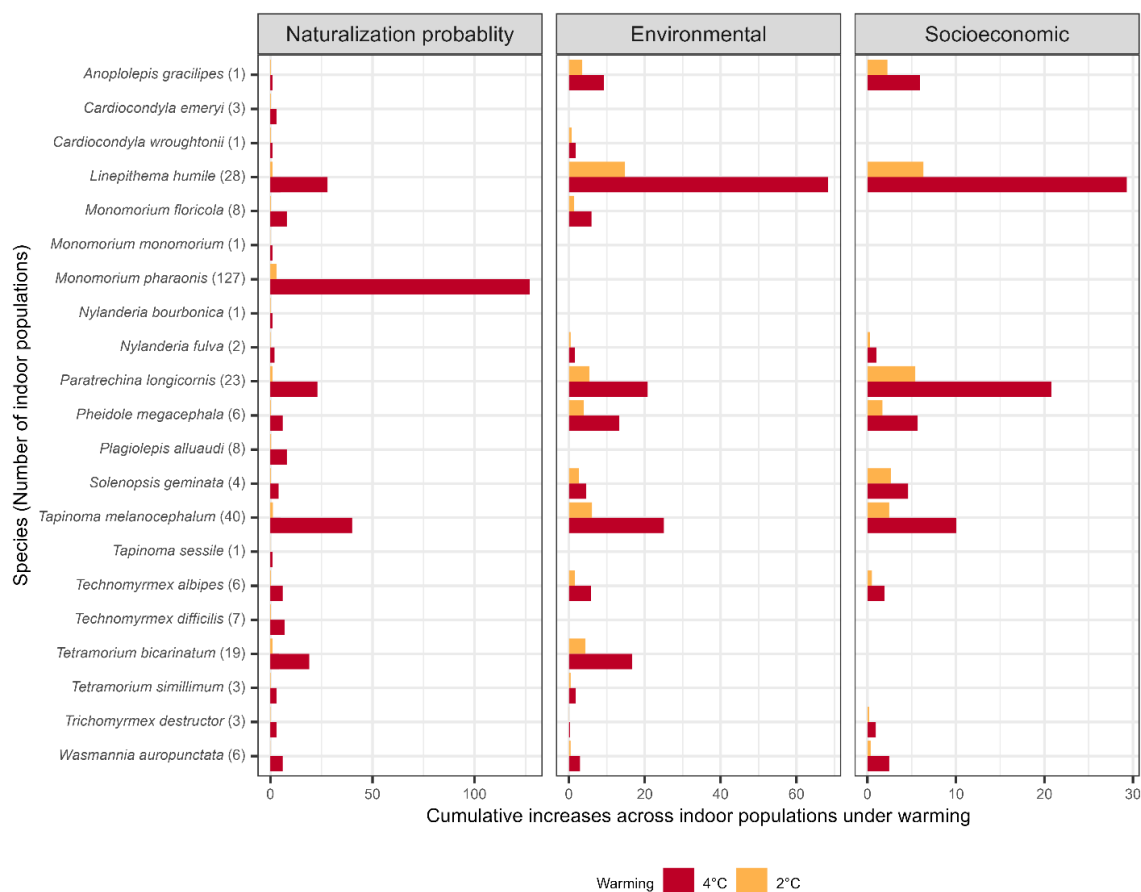
923
924 **Figure S3.** The cumulative increase in naturalization probability, environmental impacts, and
925 socioeconomic impacts associated with each harmful species across all indoor populations under
926 two warming scenarios. A larger increase indicates climate change facilitates the naturalization of
927 the species and their associated impacts more strongly. Some well-known alien ants with
928 negative impacts such as *Solenopsis invicta*, *Brachyponera chinensis* are not shown here due to
929 a lack of indoor record at present.

930
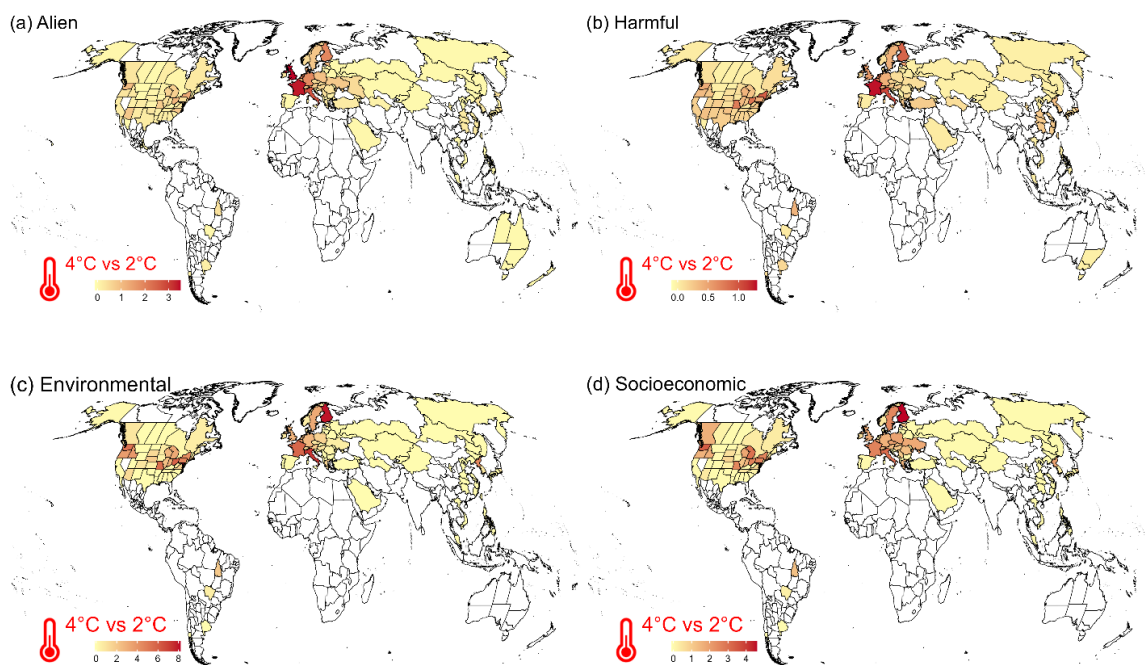
931
932 **Figure S4.** Additional gains in alien (a) and harmful species richness (b), environmental impacts
933 (c), and socioeconomic impacts (d) under 4°C warming compared to 2°C warming.

934
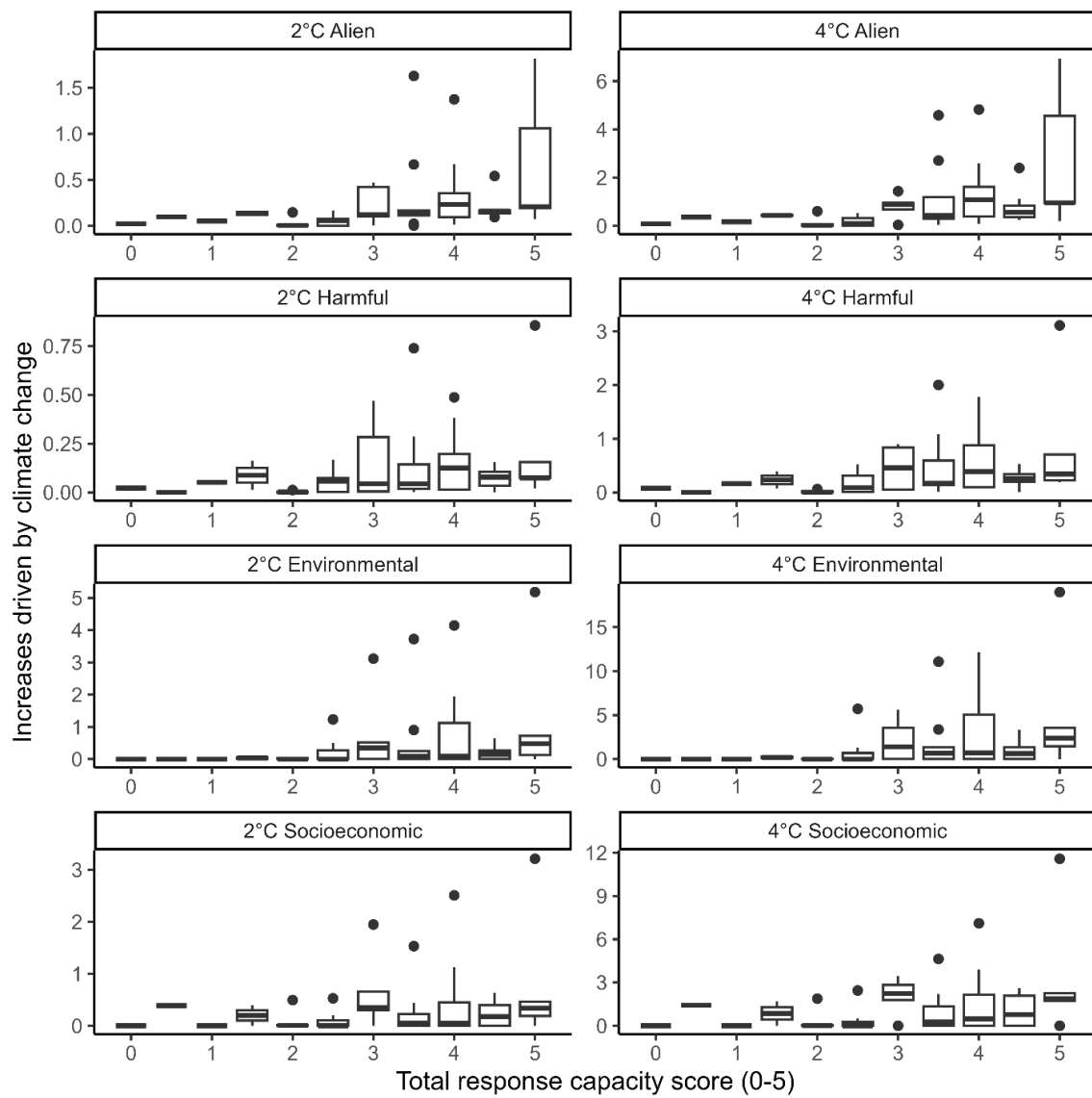
935
Figure S5. Climate change impacts across countries with different levels of response capacity (n
= 54). Climate change impacts are calculated as the sum of gain in naturalization probability.

938

Total response capacity score

939

Figure S6. Total response capacity score across different countries following Early et al. (2016).

941

942   Table S1 Species considered harmful in this study based on Gruber et al. (2022). * are species
943   included in the Global Invasive Species Database (http://www.iucngisd.org/gisd/).

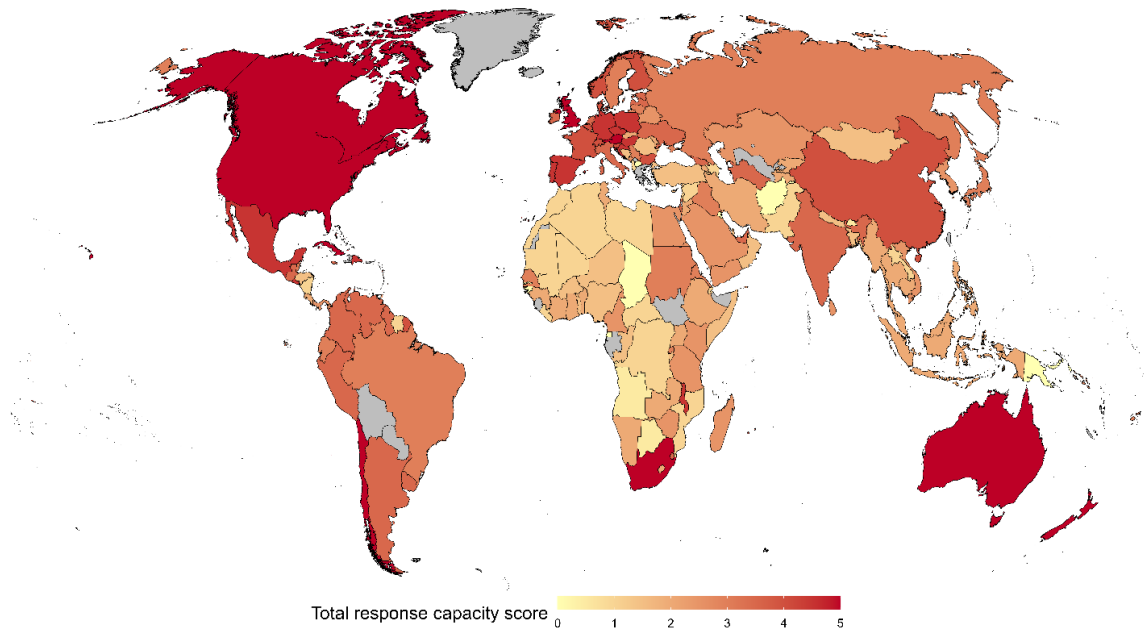| |
|---|
| *Anoplolepis custodiens* |
| *Anoplolepis gracilipes** |
| *Azteca sericeasur* |
| *Brachyponera chinensis** |
| *Camponotus conspicuus zonatus* |
| *Cardiocondyla wroughtonii* |
| *Cardiocondyla emeryi* |
| *Formica aquilonia* |
| *Formica paralugubris* |
| *Lasius neglectus** |
| *Linepithema 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** |

944

945   Table S2 Determinants on the indoor status of alien ants (n = 4,819). Significant results are
946   bolded. The reference level of habitat strata was set as species using all strata.

Full model (R^2_m = 0.43, R^2_c = 0.99)				
	β	S.E.	z	P
Intercept	69.945	86.091	0.812	0.417
Introduced water PCA1	0.748	0.656	1.141	0.254
Native water PCA1	0.158	0.402	0.393	0.694
Introduced temperature PCA1	1.873	2.087	0.898	0.369
Native temperature PCA1	**11.29**	**2.806**	**4.024**	**<0.001**
Log10(date)	-18.606	25.892	-0.719	0.472
Arboreal	1.63	2.68	0.608	0.543
Arboreal & Ground	0.116	2.727	0.043	0.966
Ground	3.225	2.514	1.283	0.2
Ground & Litter-and-soil	3.433	3.62	0.948	0.343
Litter-and-soil	3.671	2.699	1.36	0.174
Introduced water PCA1 * Native water PCA1	0.101	0.234	0.43	0.667
Introduced temperature PCA1 * Native temperature PCA1	**8.805**	**2.153**	**4.089**	**<0.001**
Simplified model (R^2_m = 0.43, R^2_c = 0.99)				
Intercept	69.845	85.529	0.817	0.414
Introduced water PCA1	0.897	0.565	1.588	0.112
Native water PCA1	0.187	0.396	0.472	0.637
Introduced temperature PCA1	1.951	2.063	0.946	0.344
Native temperature PCA1	**11.254**	**2.762**	**4.074**	**<0.001**
Log10(date)	-18.576	25.719	-0.722	0.47
Arboreal	1.598	2.639	0.606	0.545
Arboreal & Ground	0.101	2.688	0.038	0.97
Ground	3.176	2.471	1.285	0.199
Ground & Litter-and-soil	3.368	3.567	0.944	0.345
Litter-and-soil	3.632	2.654	1.368	0.171
Introduced temperature PCA1 * Native temperature PCA1	**8.804**	**2.121**	**4.15**	**<0.001**
Final model (R^2_m = 0.50, R^2_c = 0.94)				
Intercept	**7.425**	**1.709**	**4.344**	**<0.001**
Introduced temperature PCA1	0.431	1.323	0.326	0.744
Native temperature PCA1	**6.978**	**1.107**	**6.302**	**<0.001**
Introduced temperature PCA1 * Native temperature PCA1	**5**	**0.894**	**5.592**	**<0.001**

947

Table S3 Determinants of indoor status of ants, after excluding potentially undersampled regions based on three thresholds.

Excluding regions with no indoor alien populations (n=1,370; R^2_m=0.44, R^2_c=0.93)				
	β	S.E.	z	P
Intercept	100.603	66.506	1.513	0.13
Introduced water PCA1	0.589	0.457	1.287	0.198
Native water PCA1	-0.09	0.283	-0.319	0.75
Introduced temperature PCA1	2.918	1.778	1.641	0.101
Native temperature PCA1	7.442	1.417	5.252	<0.001
Log10(date)	-28.779	20.102	-1.432	0.152
Arboreal	0.815	1.918	0.425	0.671
Arboreal & Ground	0.123	1.97	0.063	0.95
Ground	2.073	1.776	1.167	0.243
Ground & Litter-and-soil	2.417	2.385	1.013	0.311
Litter-and-soil	2.704	1.903	1.421	0.155
Introduced water PCA1 * Native water PCA1	0.152	0.179	0.851	0.395
Introduced temperature PCA1 * Native temperature PCA1	**5.203**	**1.26**	**4.131**	**<0.001**
Excluding regions with ≤ 1 indoor alien populations (n=745; R^2_m=0.41, R^2_c=0.90)				
Intercept	32.472	79.631	0.408	0.683
Introduced water PCA1	0.99	0.647	1.531	0.126
Native water PCA1	-0.467	0.38	-1.228	0.219
Introduced temperature PCA1	**5.817**	**2.431**	**2.393**	**0.017**
Native temperature PCA1	**7.875**	**1.875**	**4.199**	**<0.001**
Log10(date)	-7.952	24.139	-0.329	0.742
Arboreal	0.904	2.448	0.369	0.712
Arboreal & Ground	0.218	2.533	0.086	0.931
Ground	2.316	2.274	1.019	0.308
Ground & Litter-and-soil	2.716	3.019	0.9	0.368
Litter-and-soil	3.515	2.436	1.443	0.149
Introduced water PCA1 * Native water PCA1	0.234	0.273	0.854	0.393
Introduced temperature PCA1 * Native temperature PCA1	**5.258**	**1.754**	**2.997**	**0.003**
Excluding regions with ≤ 2 indoor alien populations (n=569; R^2_m=0.52, R^2_c=0.90)				
Intercept	-51.034	85.731	-0.595	0.552
Introduced water PCA1	0.829	0.886	0.937	0.349
Native water PCA1	-0.397	0.364	-1.092	0.275
Introduced temperature PCA1	4.586	2.444	1.877	0.061
Native temperature PCA1	**8.442**	**2.078**	**4.063**	**<0.001**
Log10(date)	17.096	26.034	0.657	0.511
Arboreal	0.685	2.733	0.251	0.802

Arboreal & Ground	0.484	2.814	0.172	0.864
Ground	2.476	2.576	0.961	0.337
Ground & Litter-and-soil	1.742	3.378	0.516	0.606
Litter-and-soil	3.366	2.756	1.222	0.222
Introduced water PCA1 * Native water PCA1	0.264	0.345	0.765	0.444
Introduced temperature PCA1 * Native temperature PCA1	**5.252**	**1.916**	**2.741**	**0.006**

950

951 Table S4 Percentage of climate change impacts associated with the top-10 and -20 countries
952 under different scenarios. Climate change impacts are calculated as the sum of gain in outdoor
953 establishment probability.

2°C	Alien	Harmful	Environmental	Socioeconomic
Top-10	68.3%	67.8%	85.0%	71.9%
Top-20	82.6%	87.7%	97.5%	93.0%
4°C	Alien	Harmful	Environmental	Socioeconomic
Top-10	65.1%	63.2%	78.4%	62.3%
Top-20	83.8%	83.8%	96.1%	90.2%

954

955

956 Table S5 Percentage of highly threatened countries scored as "comprehensive" in each invasive
957 species management aspect.

2°C Alien	Threat	List	Management	Research	Monitoring
Top-10	100	90	40	80	60
Top-20	100	85	30	80	65
4°C Alien					
Top-10	100	80	30	90	70
Top-20	100	85	30	85	65
2°C Harmful					
Top-10	100	80	30	60	40
Top-20	100	85	30	75	60
4°C Harmful					
Top-10	100	90	40	70	60
Top-20	100	80	30	70	60
2°C Environmental					
Top-10	100	80	30	90	60
Top-20	100	85	30	85	60
4°C Environmental					
Top-10	100	70	30	90	50
Top-20	100	85	30	80	65
2°C Socioeconomic					
Top-10	100	80	40	70	50
Top-20	95	80	25	75	55
4°C Socioeconomic					
Top-10	100	70	30	90	60
Top-20	100	80	30	80	55

958

959

Table S6 Missing genera from the phylogenetic tree and their placement. If possible, we placed each missing genus according to molecular phylogeny data. If not, they were assigned to the closest genus based on previous placement before they were upgraded to genus level. For example, *Erromyrma* was previously placed in *Monomorium*.

Missing genus	Sister1	Sister2	References
Chelaner	*Austromorium*		(1)
Colobopsis	*Calomyrmex*	*Opisthopsis*	(2)
Erromyrma	*Monomorium*		(3)
Lepisiota	*Prenolepis*	*Plagiolepis*	(4)
Lioponera	*Cerapachys*		(5)
Ooceraea	*Cerapachys*		(5)
Parasyscia	*Cerapachys*		(5)
Parvaponera	*Cryptopone*		(6)

References for Table S6

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