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2 **Main Manuscript for:**
3 Historical plant introductions predict current insect invasions
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44   Supplementary materials and methods

Abstract:

Thousands of insect species have been introduced outside of their native ranges, and some of them strongly impact ecosystems and human societies. Because a large fraction of insects feed on or are associated with plants, non-native plants provide habitat and resources for invading insects, thereby facilitating their establishment. Furthermore, plant imports represent one of the main pathways for accidental non-native insect introductions. Here, we tested the hypothesis that plant invasions precede and promote insect invasions. We found that geographical variation in current non-native insect flows were best explained by non-native plant flows dating back to 1900 rather than by more recent plant flows. Interestingly, non-native plant flows were a better predictor of insect invasions than potentially confounding socio-economic variables. Based on the observed time lag between plant and insect invasions, we estimated that the global insect invasion debt consists of 3,442 region-level introductions, representing a potential increase of 35% of insect invasions. This debt was most important in the Afrotropics, the Neotropics and Indomalaya, where we expect a 10 to 20-fold increase in discoveries of new non-native insect species. Overall, our results highlight the strong link between plant and insect invasions, and show that limiting the spread of non-native plants might be key to preventing future invasions of both plants and insects.

Significance statement:

Invasive insects severely impair ecosystem functioning and impact human societies. It is therefore urgent to better predict and prevent future invasions. Using statistical models, we show that non-native plant introductions are a major driver of insect invasions, and that insect invasions lag behind plant invasions. In the near future, new insect invasions are estimated to increase by 35% worldwide based on recent non-native plant introductions. The Afrotropics, the Neotropics and Indomalaya are the regions most at risk of future invasions. Our results highlight that limiting the introduction and spread of non-native plants will be key to preventing future insect invasions.

Main text:

Introduction

With increasing globalization, many species are transported and introduced outside of their native range, where they sometimes succeed in establishing self-sustaining populations. Some of these non-native species become highly abundant and severely impact ecosystems and human societies (1). These species are referred to as invasive species. With now more than 7,000 species established outside of their native range, insects outnumber all other non-native animals (2), and some insects are among the most damaging invaders worldwide (3). Insects are evolutionarily extremely successful and diverse. They include herbivores, predators, pollinators, and detritivores, and are major components of every biome with the exception of most marine habitats. Invasive insects have a wide range of ecological impacts, outcompeting native species, disrupting key insect-plant mutualisms, affecting native seed dispersers, changing native pollination services (4) and potentially causing species extinction (5). Many invasive insects are also important pests damaging agricultural and ornamental plants (6) as well as forests (7). A striking example is the box tree moth, *Cydalima perspectalis*, which was accidentally introduced in Europe and threatens Buxus trees all over the continent (8). Non-native insects can also spread infectious diseases in humans and livestock (9, 10). The two invasive mosquitoes *Aedes aegypti* and *Aedes albopictus* are efficient vectors of several human arboviral diseases such as dengue, zika, chikungunya and yellow fever, and the distribution of these two species will continue to expand in the coming decades (11). Overall, the economic cost of non-native insects is estimated to exceed US$70.0 billion per year globally (12) and is likely to increase in the future as many new insect invasions can be expected due to ongoing global exchanges. It is therefore urgent to better understand the drivers of insect introductions to better predict future invasions and limit their impact.

One possible predictor of future insect invasions are current plant invasions. Plant introductions may precede insect invasions because insects have tight relationships with plants, with many insect species feeding or living on plants (13). Consequently, many insects are transported accidentally on plant products (14–16). The trade of live plants for horticultural and ornamental purposes is therefore an important pathway of non-native insect introductions (17–20). In Great Britain, almost 90% of invertebrate plant pest introductions are associated with the plant trade, in particular with ornamental plants (18). Non-native plant diversity is also an important driver of insect invasions (21) as they can facilitate the establishment and spread of non-native insect species, in particular those that rely on plants as hosts (22–25). Non-native plants can also promote invasions of pollinators and plant visitors (26, 27). While it has been shown that areas with higher numbers of native and non-native plant species also harbor higher numbers of invasive insects (21), it remains unknown if insect invasions follow plant invasions. If this hypothesis is correct, current plant invasions might be used to predict future insect invasions.

Time lags between drivers of invasions and actual non-native species establishment have been previously identified. For many taxa, the current distribution of non-native species is better explained by socio-economic indicators from the year 1900 than to those from 2000 (28), suggesting an important historical legacy (29). This time lag between cause and effect suggests that socio-economic activities lead to an "invasion debt" (28), caused by past socio-economic processes. Invasions may be delayed when a species has been present in low numbers in its introduced range for a long time before starting to spread. For example, this may happen if past environmental conditions did not yet allow the species to spread. This is different from "future invasions" which refers to introduction of species by future trade activities. Here, we tested the predictive power of lagged vs. current non-

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123 native plant flows (from years 1800 to 2010) for non-native insect invasions at a global scale. We
124 built generalized linear models of non-native insect flows between biogeographic regions, using data
125 of non-native plant and insect first record dates per region and information on their native range. As
126 global trade dynamics strongly influence biological invasions (30–32), we also included lagged and
127 current trade flows in the models. In this analysis, we i) tested the predictive power of lagged vs.
128 current non-native plant flows and confounding variables on insect invasions, ii) quantified the time
129 lag between plant and insect invasions and iii) estimated insect invasion debt in each biogeographic
130 region based on the observed time lag.

Results

Patterns of insect and plant invasions

The greatest number of recorded insect introductions so far has occurred in the Nearctic, Oceania (mostly Hawaii), Europe and Australasia (Figure 1A). In comparison, records of non-native insect species are much more limited in the Asian Palearctic, the Neotropics, the Afrotropics and Indomalaya. But non-native insect richness in these regions is likely to be largely underestimated as these regions are under-sampled (33). Similar invasion patterns were observed for plants through 1900, with Europe, the Nearctic and Australasia being the main recipients of historical plant introductions (Figure 1C). Since 1900, many non-native plant species have been recorded in the Afrotropics, Oceania and Asia (Figure 1B). The current distribution of non-native insects is therefore more correlated to the distribution of non-native plants from 1900 (linear model $R^2 = 0.58$) rather than 2010 (linear model $R^2 = 0.49$).

Time lag between plant and insect invasions

We used generalized linear mixed models (GLMMs) to test the predictive power of historical and current non-native plant flows on non-native insect flows between biogeographic regions. We found that current non-native insect flows were best explained by non-native plant flows up to 1900, as indicated by the lowest AIC (AIC = 627.5; Nakagawa's $R^2 = 0.95$ (34), Figure 2A), rather than by more recent plant flows. The relationship between plant and insect flows is shown in Supplementary figure 1. An AIC difference (ΔAIC) > 2 indicates that the weaker model has low comparative support, and models with ΔAIC > 10 have no support (35). Here, the model with plant flows through 1900 was significantly better than the model with plant flows through 2010 (ΔAIC = 11.7). Accounting for unequal sampling between regions did not change these dynamics (Supplementary figure 3A). We then tested for the potentially confounding effect of trade flows on insect invasions. We found a similar time lag between plant and insect flows when trade flows of plant products and general trade flows of 1900 and 2010 were included in the models (Figure 2A, Supplementary figure 3B, Supplementary figure 4A). Finally, non-native plant flows were a better predictor of non-native insect invasions than general trade flows and plant product trade flows (Figure 2B, Supplementary figure 4B).

Insect invasion debt

We estimated insect invasion debt in each biogeographic region based on the observed time lag between plant and insect flows. We used the coefficient of the best linear model (i.e., with non-native plant flows of 1900) to predict the expected non-native insects flows between regions given the total flows of plant observed until 2010. We then computed the insect invasion debt as the difference between the expected flows of non-native insects and the observed flows (Figure 3B). We found a global debt of 3,442 insect introductions across all biogeographic regions (Figure 3B). So far, a total of 9,952 insect introductions (7,592 species) have been recorded from the eight regions (Figure 3A). The number of known insect invasions can therefore be expected to increase by 35% worldwide in the near future. The invasion debt was greatest in the Afrotropics (869 species), the Neotropics (809 species) and Indomalaya (776 species). Few non-native insects have currently been recorded in these regions. Our results suggest that the number of non-native insect species is expected to increase almost 10-fold in the Afrotropics and the Neotropics, and about 20-fold in Indomalaya over the coming years (Figure 3). The smallest debt was found for Oceania (the estimated debt is null for this region) and the Nearctic (16 species), which have already received many non-native insect species. The debt was relatively high in the European Palearctic (417 species) and Australasia (317 species)

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181 despite the fact that many non-native insects have already been introduced in these regions (Figure
182 3). Finally, the Neotropics are expected to be the greatest source of insect invasions in the future (904
183 exported species), followed by the European Palearctic (732 species, Figure 3B).

Discussion

Current inter-regional non-native insect flows are best explained by non-native plant flows through 1900 compared to more recent plant flows, indicating that plant introductions precede invasions of non-native insect species that use these plants as host (24, 25, 36). There are several potential explanations for the extensive time lag. For example, non-native host plants must first increase in abundance and start spreading before non-native insects are able to establish and spread in turn. The local spread of non-native plants can take time. In addition, repeated introductions of a given plant species are probably necessary before an insect species that is sometimes transported on this plant species (14–16, 19) reaches a sufficient propagule pressure to establish a self-sustaining population. Furthermore, our analyses included all non-native insect species belonging to various feeding groups, and only the spread of herbivores (25) and pollinators (26, 27) may be directly facilitated by plants. However, subsequently, the establishment of herbivores and pollinators promotes the invasion of predators and parasitoids. This "trickle up" effect of trophic influences may also contribute to time lags between plant and insect invasions. The observed time lag could also partly be explained by the fact that establishment of new insect species may be recorded later than for plants because plants tend to be better sampled than insects. Indeed, insects are highly underrepresented in biodiversity databases, while plants are usually well sampled (37). Established insects might stay at low abundance for several decades, a phenomenon described as "sleeper populations" (38), and might therefore remain undetected for an extended period (38, 39). For example, MacLaughlin *et al.* (40) reported a median delay between establishment and discovery of about 80 years for plant-feeding Hemiptera which are small and easily overlooked. This suggests that the actual time lag between plant and insect esatblishment may be shorter than we observed. Non-native plants are also often introduced intentionally for horticultural and ornamental purposes (41, 42), while insects are mostly transported accidentally, as contaminants or stowaways (43, 44), and might therefore be more difficult to detect as their presence may be less expected. This again suggests that we may overestimate the true time lag between plant and insect invasions.

Using this observed time lag between plant and insect establishment, we estimated the insect invasion debt in each biogeographic region, which refers to insect invasions caused by historical plant introductions, but that have not occurred yet. We found a substantial debt of 3,442 region-level insect introductions worldwide, suggesting a potential increase of 35% of new reports of insect invasions over the coming years. While insect invasions have so far mainly been recorded in the European Palearctic, Nearctic, Australasia and Oceania, the most important debts were found for the Afrotropics (869 species), the Neotropics (809 species) and Indomalaya (776 species). The number of discoveries of insect introductions is expected to increase almost 10-fold in the Afrotropics and the Neotropics, and 20-fold in Indomalaya. This is of particular concern given that the number of plant invasions in emerging economies is also predicted to continue accelerating in the coming years (45), which could further promote future insect invasions. It should however be emphasized that the non-native insect fauna already established in these regions is largely underestimated as these regions tend to be poorly sampled (33). For instance, a high proportion of insect species intercepted by biosecurity services at ports of entry and arriving from Africa and South America are not yet recorded as established in these regions (46). The insect invasion debt may therefore be partly attributed to species that are already established but not recorded, and partly to future species establishments. A previous study also predicted an increase of arthropod invasions by 2050 in Africa, South America and Tropical Asia (47), yet at a slower rate than what our results suggest. However, this previous study used records of historical arthropod invasions to anticipate future trajectories, and might therefore underestimate future invasions due to the incompleteness of non-native arthropod records in these regions. It should also be noted that our estimate of insect invasion debt is based on the number of plant introductions,

234 but other factors such as biosecurity measures and national policies on imports also influence insect
235 invasions. Moreover, we assume that the slope of the relationship between plant and insect invasions
236 is constant overtime. Our analysis therefore provides a first assessment of insect invasion debt per
237 region, but further research is required to precisely estimate invasion risk as well as the insect taxa
238 most likely to be introduced in the different regions.

239
240 Although a high number of insects have already established in the European Palearctic and
241 Australasia, we found an important debt in these regions. Most future insect introductions in the
242 European Palearctic are expected to be intra-continental, which is consistent with the many intra-
243 continental plant introductions observed in this region (Supplementary figure 2) (48). The debt for
244 Oceania was null, and very small for the Nearctic, as many insects have already established and have
245 been recorded in these regions. But this does not indicate that insect species will no longer be
246 introduced in these regions, since importations of commodities and the introduction of new non-
247 native plants in the future are likely to promote new insect invasions, if the potential source pool of
248 emergent non-native species is not depleted. Previous research has indicated that this should not be
249 the case for non-native insects in North America (47), while plant invasions may saturate in this region
250 (47), suggesting that, beyond the estimated invasion debt, many new non-native insects may fail to
251 establish.

252
253 Many insects from the European Palearctic have been introduced to the Nearctic. In comparison,
254 fewer insects have been introduced in the opposite direction. Mattson *et al. (49)* argued that there
255 may be fewer niches for invasive insects in Europe due to the lower host plant diversity in this region
256 caused by the Pleistocene/Holocene glaciations. Although this hypothesis is still in dispute (20), it
257 could explain this asymmetry in insect invasions. However, a similar asymmetry can be observed for
258 non-native plants (Supplementary figure 2), with more introductions from the European Palearctic to
259 the Nearctic than in the opposite direction, possibly due to European colonialism (29). Our results
260 therefore suggest that the asymmetry in insect invasions might be driven by the asymmetry in plant
261 invasions.

262
263 Our analysis highlights the role of plant invasions in driving insect invasions. Interestingly, we found
264 that general trade flows and plant related trade flows did not explain additional variation in insect
265 invasions once non-native plant flows were included in the model. This shows that although global
266 trade is a strong driver of biological invasions (30–32), it cannot explain all geographical variation in
267 insect invasion frequencies, and suggests that geographical variation in habitat invasibility plays an
268 important role (21). Previous invasions might be important in determining invasion dynamics.

269
270 A potential limitation of our approach is that it does not account for "bridgehead effects". The
271 bridgehead effect is a phenomenon of secondary spread where non-native insects arrive to a new
272 region from a previously invaded region, rather than directly from the native range (50). This
273 phenomenon has a strong impact on the spread of non-native insects (50–53). If a high proportion of
274 species are established in several continents, bridgehead effects tend to be more frequent which can
275 distort our global view of non-native species flows (54). But in this analysis, the majority of non-
276 native insect and plant species were recorded in only one biogeographic region (Supplementary figure
277 5), which suggests that recorded non-native species flows largely reflect actual introduction routes.
278 Moreover, it appears that insects follow similar invasion patterns as the plants with which they have
279 co-evolved with in their native range, regardless if they were introduced directly from their native
280 range or from a bridgehead region. Our aim was not to predict the exact future spread routes, but
281 rather to anticipate future flows of non-native insects from donor to recipient regions.

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283 Our analysis revealed an important time lag between plant and insect invasions at a global scale.
284 Further research could investigate this time lag at the scale of individual insect species for which the
285 host plant species are known. Our data did not include georeferenced records and therefore we cannot
286 confirm that non-native insects and plants are actually co-occurring, but previous studies suggest that
287 it is very likely to be the case (25–27). Future studies might also assess the effect of non-native plants
288 which have been planted for agriculture, forestry or horticulture but have not managed to establish
289 populations in the wild yet. These species are not represented in our data, but may also contribute to
290 the spread of non-native insects specializing on those plants (24, 55). Similarly, many invasive insects
291 may be associated with ornamental plants used in urban landscapes (56).
292
293 Time lags may vary among taxonomic groups, feeding guilds and also among regions. Understanding
294 what drives these time lags would inform efforts to better predict and manage future insect invasions.
295 Future research could also investigate the effect of non-native plant abundance, rather than just
296 species richness, on non-native insect establishment. It is likely that the probability of insect
297 establishment increases as non-native plants spread and increase in abundance in a given region.
298
299 Overall, we have shown that global insect invasions lag behind plant invasions. Given patterns of
300 recent plant introductions, insect invasions are expected to rise in tropical regions, which could
301 strongly impact local economies and threaten biodiversity. Our study highlights that non-native plants
302 can have indirect environmental consequences by facilitating insect invasions. Including the risk of
303 insect introduction in invasion risk screening tools might therefore be necessary when assessing the
304 potential impact of non-native plants. Targeting plant imports (57), and limiting the establishment and
305 spread of non-native plants might also help to reduce invasions of insect in the future.
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Materials and methods

Non-native species flows

Records of insect establishments and plant naturalizations were compiled for each of the eight world biogeographic regions (Asian Palearctic, European Palearctic, Afrotropic, Neotropic, Indomalaya, Nearctic, Australasia and Oceania) using a system modified from Wallace's designation and snapped to country borders (Supplementary figure 6). We extracted data of non-native insect and vascular plant first record dates per country or region from online datasets (2, 58–61). We also used information on insect and plant non-native range from the Global Register of Introduced and Invasive Species (GRIIS) (62) together with dated occurrences from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org) (63, 64) to extract additional non-native species first records. We cleaned species synonyms using the R package *taxizedb (65)* based on the GBIF taxonomic backbone. We then merged these datasets of non-native species first records. When the different data sources indicated different first records dates for a given species in a given country, we used the earliest date. It resulted in 16,486 establishment records of 7,592 non-native insect species, and 54,020 naturalization records of 10,560 non-native plant species made prior to 2010. We did not include data from the most recent years (2011-present) as they are incomplete because of the delay in the publication of new non-native species records (2, 66). Most of the extracted first records were at the country level. As we analyzed species flows at the region level, we only kept the first record date per biogeographic region for each non-native insect and plant species.

Data on insect native ranges were sourced from Turner *et al.* (60). Data on plant native ranges were extracted from the World Checklist of Selected Plant Families (67). We thus obtained information on native ranges of 90% of non-native insect and 85% of non-native plant species. We then used the non-native species first records per biogeographic region and their native ranges to reconstruct flows of non-native species between pairs of origin and recipient region. Flows were quantified as the number of species introduced from one region to another region. When a species was native to more than one region, we weighted the flows of this species by the number of regions where it is native from.

Trade data

Data on general trade flows were extracted from the TRADHIST database (68). TRADHIST gathers more than 1.9 million bilateral trade flows between 319 administrative entities from 1827 to 2014. It includes data from various sources such as government publications, books and academic articles. We computed general trade flows between biogeographic regions as the sum of trade values between countries of each region pair for the years 1900 and 2010. Data on plant product trade flows for the year 2010 were extracted from the United Nations Comtrade database (https://comtradeplus.un.org) using the R package *comtradr* (69). We followed the same traded commodity classification as Fenn-Moltu *et al.* (15) for plant products.

Modeling

Statistical models were used to test the role of various candidate predictors for their ability to explain current (2010) insect flows among biogeographical regions. We first tested the predictive power of historical and current non-native plant flows on non-native insect flows, using generalized linear mixed models (GLMMs) with a zero truncated negative binomial distribution. Current insect flows were computed as cumulative species invasions between each of the 64 pairs of biogeographic regions

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recorded for years prior to 2010. Plant flows were calculated for each of the same pairs of regions but as cumulative naturalizations in decadal steps, from 1800 to 2010. We did not investigate the association between individual plant and insect species, we tested the correlation between the number of insect and plant species that were moved from a donor to a recepient region.

We used an iterative approach: we first fitted a model of current insect flows (i.e., cumulative flows of insects until 2010) as a function of non-native plant flows until year 1800 (i.e. cumulative flows of plants until 1800; log-transformed to normalize their distribution). We then fitted separate models for each subsequent decade starting with 1810 and ending with 2010, using the cumulative non-native plant flows until each decade as the predictive variable (log-transformed), while keeping the same response variable across all the models (i.e., insect flows until 2010). We did not test plant flows prior to 1800 because few non-native plants have been recorded before that date (2). This resulted in 22 GLMMs predicting current insect flows as a function of plant flows cut-off at each decade (from 1800 to 2010). We also included origin and destination of the non-native species flows as random effects on the intercept for each model. The models were evaluated using AIC scores.

For each decade x (with $1800 \leq x \leq 2010$), the model can be summarised as:

Insect flows (through 2010) $\sim$ Plant flows (through year x) + (1|origin) + (1|destination)

To test for the predictive power of lagged and current trade flows on non-native insect flows, we then repeated the same modeling approach, but added general trade flows (log-transformed) as a predictor in the models. We tested the effect of general trade flows of 1900 and 2010. As trade data were not available for all regions for 1900, 13 pairs of origin-destination regions were removed from the models with trade flows of 1900. To allow comparison between the different modeling approaches, we also reran the previous models (i.e., without trade flows and with trade flows of 2010) after removing the same 13 pairs of biogeographic regions from the models. As insects are mostly transported on plant products (14, 15), we also tested the effect of plant product trade flows of 2010 on insect invasions, using the same modeling approach. We did not test the effect of lagged plant product trade flows as detailed data on traded commodities are only available for the recent years.

Another important factor influencing observed patterns of invasions is sampling effort (31, 70). To control for unequal sampling between regions, we repeated the same modeling approach but included, as an additional predictor variable, the number of all native insect occurrences per square kilometer as a proxy for sampling effort (see Supplementary materials and methods).

Estimating insect invasion debt

We used the coefficient of the best model (i.e., with non-native plant flows until 1900, Figure 2A) to predict the expected flows of non-native insects given the total flows of non-native plants observed until 2010. We then subtracted the current non-native insect flow (i.e., the total flow of non-native insect species discovered up to 2010) from the predicted flow of non-native insects, and thereby obtained the insect invasion debt. We therefore used a single predictor, current non-native plant flows, to estimate the insect invasion debt. We also assume that the slope of the relationship between plant and insect flows is constant overtime.

All analyses were performed with R 4.1.2. (71).

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413 **References:**

1. P. Pyšek, *et al.*, Scientists' warning on invasive alien species. *Biological Reviews* **95**, 1511–1534 (2020).

2. H. Seebens, *et al.*, No saturation in the accumulation of alien species worldwide. *Nature Communications* **8**, 1–9 (2017).

3. Global Invasive Species Database (2022) (December 12, 2022).

4. M. P. Hill, S. Clusella-Trullas, J. S. Terblanche, D. M. Richardson, Drivers, impacts, mechanisms and adaptation in insect invasions. *Biological Invasions 2016 18:4* **18**, 883–891 (2016).

5. M. Kenis, *et al.*, Ecological effects of invasive alien insects. *Biological Invasions* **11**, 21–45 (2009).

6. C. M. Oliveira, A. M. Auad, S. M. Mendes, M. R. Frizzas, Economic impact of exotic insect pests in Brazilian agriculture. *Journal of Applied Entomology* **137**, 1–15 (2013).

7. S. Fei, R. S. Morin, C. M. Oswalt, A. M. Liebhold, Biomass losses resulting from insect and disease invasions in US forests. *Proceedings of the National Academy of Sciences of the United States of America* **116**, 17371–17376 (2019).

8. A. Bras, *et al.*, The fast invasion of Europe by the box tree moth: an additional example coupling multiple introduction events, bridgehead effects and admixture events. *Biol Invasions* **24**, 3865–3883 (2022).

9. P. S. Mellor, J. Boorman, M. Baylis, Culicoides biting midges: Their role as arbovirus vectors. *Annual Review of Entomology* **45**, 307–340 (2000).

10. S. Leta, *et al.*, Global risk mapping for major diseases transmitted by Aedes aegypti and Aedes albopictus. *International Journal of Infectious Diseases* **67**, 25–35 (2018).

11. M. U. G. Kraemer, *et al.*, Past and future spread of the arbovirus vectors Aedes aegypti and Aedes albopictus. *Nature Microbiology 2019 4:5* **4**, 854–863 (2019).

12. C. J. A. Bradshaw, *et al.*, Massive yet grossly underestimated global costs of invasive insects. *Nature Communications* **7**, 1–8 (2016).

13. D. R. Strong, J. H. Lawton, S. R. Southwood, *Insects on plants. Community patterns and mechanisms.* (Blackwell Scientific Publicatons, 1984) (December 14, 2022).

14. N. Meurisse, D. Rassati, B. P. Hurley, E. G. Brockerhoff, R. A. Haack, Common pathways by which non-native forest insects move internationally and domestically. *Journal of Pest Science* **92**, 13–27 (2019).

15. G. Fenn-Moltu, *et al.*, Alien insect dispersal mediated by the global movement of commodities. *Ecological Applications*, e2721 (2022).

16. S. Ollier, C. Bertelsmeier, Precise knowledge of commodity trade is needed to understand invasion flows. *Frontiers in Ecology and the Environment* **20**, 467–473 (2022).

17. M. Kenis, W. Rabitsch, M. A. Auger-Rozenberg, A. Roques, How can alien species inventories and interception data help us prevent insect invasions? *Bulletin of Entomological Research* **97**, 489–502 (2007).

18. R. M. Smith, *et al.*, Recent non-native invertebrate plant pest establishments in Great Britain: origins, pathways, and trends. *Agricultural and Forest Entomology* **9**, 307–326 (2007).

19. A. M. Liebhold, E. G. Brockerhoff, L. J. Garrett, J. L. Parke, K. O. Britton, Live plant imports: The major pathway for forest insect and pathogen invasions of the US. *Frontiers in Ecology and the Environment* **10**, 135–143 (2012).

20. A. Roques, *et al.*, Are Invasive Patterns of Non-native Insects Related to Woody Plants Differing Between Europe and China? *Frontiers in Forests and Global Change* **2** (2020).

21. A. M. Liebhold, *et al.*, Plant diversity drives global patterns of insect invasions. *Scientific Reports* **8**, 1–5 (2018).

22. S. J. Bacon, A. Aebi, P. Calanca, S. Bacher, Quarantine arthropod invasions in Europe: The role of climate, hosts and propagule pressure. *Diversity and Distributions* **20**, 84–94 (2014).

23. D. P. Bebber, T. Holmes, S. J. Gurr, The global spread of crop pests and pathogens. *Global Ecology and Biogeography* **23**, 1398–1407 (2014).

24. B. P. Hurley, *et al.*, Increasing numbers and intercontinental spread of invasive insects on eucalypts. *Biological Invasions* **18**, 921–933 (2016).

25. R. Mally, *et al.*, Non-native plant drives the spatial dynamics of its herbivores: the case of black locust (Robinia pseudoacacia) in Europe. *NeoBiota* **69**, 155–175 (2021).

26. C. L. Morales, M. A. Aizen, Does Invasion of Exotic Plants Promote Invasion of Exotic Flower Visitors? A Case Study from the Temperate Forests of the Southern Andes. *Biological Invasions* **4**, 87–100 (2002).

27. F. E. Fontúrbel, *et al.*, Do exotic plants and flower colour facilitate bumblebee invasion? Insights from citizen science data. *Flora* **298**, 152200 (2023).

28. F. Essl, *et al.*, Socioeconomic legacy yields an invasion debt. *Proceedings of the National Academy of Sciences of the United States of America* **108**, 203–207 (2011).

29. B. Lenzner, *et al.*, Naturalized alien floras still carry the legacy of European colonialism. *Nat Ecol Evol*, 1–10 (2022).

30. C. Bertelsmeier, S. Ollier, A. Liebhold, L. Keller, Recent human history governs global ant invasion dynamics. *Nature Ecology and Evolution* **1**, 0184 (2017).

31. A. Bonnamour, J. M. W. Gippet, C. Bertelsmeier, Insect and plant invasions follow two waves of globalisation. *Ecology Letters* **24**, 2418–2426 (2021).

32. P. E. Hulme, Unwelcome exchange: International trade as a direct and indirect driver of biological invasions worldwide. *One Earth* **4**, 666–679 (2021).

33. A. C. Hughes, *et al.*, Sampling biases shape our view of the natural world. *Ecography* **44**, 1259–1269 (2021).

34. S. Nakagawa, P. C. D. Johnson, H. Schielzeth, The coefficient of determination R2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. *Journal of The Royal Society Interface* **14**, 20170213 (2017).

35. K. P. Burnham, D. R. Anderson, Multimodel inference: Understanding AIC and BIC in model selection. *Sociological Methods and Research* **33**, 261–304 (2004).

36. S. F. Ward, A. M. Liebhold, S. Fei, Variable effects of forest diversity on invasions by non-native insects and pathogens. *Biodivers Conserv* **31**, 2575–2586 (2022).

37. J. Troudet, P. Grandcolas, A. Blin, R. Vignes-Lebbe, F. Legendre, Taxonomic bias in biodiversity data and societal preferences. *Sci Rep* **7**, 9132 (2017).

38. M. J. Spear, J. R. Walsh, A. Ricciardi, M. Jake, V. Zanden, The Invasion Ecology of Sleeper Populations: Prevalence, Persistence, and Abrupt Shifts. *BioScience* **71**, 357–369 (2021).

39. J. R. Walsh, E. J. Pedersen, M. J. Vander Zanden, Detecting species at low densities: a new theoretical framework and an empirical test on an invasive zooplankton. *Ecosphere* **9**, e02475 (2018).

40. M. J. MacLachlan, A. M. Liebhold, T. Yamanaka, M. R. Springborn, Hidden patterns of insect establishment risk revealed from two centuries of alien species discoveries. *Science Advances* **7**, eabj1012 (2021).

41. M. van Kleunen, *et al.*, The changing role of ornamental horticulture in alien plant invasions. *Biological Reviews* **93**, 1421–1437 (2018).

42. M. van Kleunen, *et al.*, Economic use of plants is key to their naturalization success. *Nature Communications 2020 11:1* **11**, 1–12 (2020).

43. W. C. Saul, *et al.*, Assessing patterns in introduction pathways of alien species by linking major invasion data bases. *Journal of Applied Ecology* **54**, 657–669 (2017).

44. J. M. W. Gippet, A. M. Liebhold, G. Fenn-Moltu, C. Bertelsmeier, Human-mediated dispersal in insects. *Current Opinion in Insect Science* **35**, 96–102 (2019).

45. H. Seebens, *et al.*, Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology* **21**, 4128–4140 (2015).

46. H. F. Nahrung, A. J. Carnegie, Border interceptions of forest insects established in Australia: intercepted invaders travel early and often. *NeoBiota* **64**, 69–86 (2021).

47. H. Seebens, *et al.*, Projecting the continental accumulation of alien species through to 2050. *Global Change Biology* **27**, 970–982 (2021).

48. M. van Kleunen, *et al.*, Global exchange and accumulation of non-native plants. *Nature 2015 525:7567* **525**, 100–103 (2015).

49. W. Mattson, H. Vanhanen, T. Veteli, S. Sivonen, P. Niemelä, Few immigrant phytophagous insects on woody plants in Europe: legacy of the European crucible? *Biol Invasions* **9**, 957–974 (2007).

50. E. Lombaert, *et al.*, Bridgehead Effect in the Worldwide Invasion of the Biocontrol Harlequin Ladybird. *PLoS ONE* **5**, e9743 (2010).

51. C. Bertelsmeier, L. Keller, Bridgehead Effects and Role of Adaptive Evolution in Invasive Populations. *Trends in Ecology & Evolution* **33**, 527–534 (2018).

52. C. Bertelsmeier, *et al.*, Recurrent bridgehead effects accelerate global alien ant spread. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 5486–5491 (2018).

53. A. J. Blumenfeld, E. L. Vargo, Geography, opportunity and bridgeheads facilitate termite invasions to the United States. *Biological Invasions* **22**, 3269–3282 (2020).

54. C. Bertelsmeier, S. Ollier, Bridgehead effects distort global flows of alien species. *Diversity and Distributions* **27**, 2180–2189 (2021).

55. F.-H. Wan, N.-W. Yang, Invasion and Management of Agricultural Alien Insects in China. *Annu. Rev. Entomol.* **61**, 77–98 (2016).

56. S. Bella, New alien insect pests to Portugal on urban ornamental plants and additional data on recently introduced species. *Annales de la Société entomologique de France (N.S.)* **49**, 374–382 (2013).

57. R. Eschen, *et al.*, International variation in phytosanitary legislation and regulations governing importation of plants for planting. *Environmental Science & Policy* **51**, 228–237 (2015).

58. H. F. Nahrung, A. J. Carnegie, Non-native Forest Insects and Pathogens in Australia: Establishment, Spread, and Impact. *Frontiers in Forests and Global Change* **3** (2020).

59. A. M. Liebhold, *et al.*, Invasion disharmony in the global biogeography of native and non-native beetle species. *Diversity and Distributions* **27**, 2050–2062 (2021).

60. R. Turner, R. Blake, A. M. Liebhold, International Non-native Insect Establishment Data (0.1) [Data set]. Zenodo. (2021) https://doi.org/10.5281/ZENODO.5245302.

61. R. Mally, *et al.*, Moths and butterflies on alien shores: Global biogeography of non-native Lepidoptera. *Journal of Biogeography* **49**, 1455–1468 (2022).

62. S. Pagad, P. Genovesi, L. Carnevali, D. Schigel, M. A. McGeoch, Introducing the Global Register of Introduced and Invasive Species. *Scientific Data* **5**, 1–12 (2018).

63. GBIF.org, GBIF Insect Occurrence Download (2021) https:/doi.org/https://doi.org/10.15468/dl.8bw6hc (July 28, 2022).

64. GBIF.org, GBIF Vascular plant Occurrence Download (2021) https:/doi.org/https://doi.org/10.15468/dl.awwnws (July 28, 2022).

65. S. Chamberlain, Z. Arendsee, taxizedb: Tools for Working with "Taxonomic" Databases. R package version 0.3.0. (2021) (March 1, 2021).

66. R. Smith, *et al.*, Non-native invertebrate plant pests established in Great Britain: An assessment of patterns and trends. *Plant Protection and Plant Health in Europe: Introduction and Spread of Invasive Species. BCPC Symposium Proceedings* **81** (2005).

67. WCSP, World Checklist of Selected Plant Families. Facilitated by the Royal Botanic Gardens, Kew. *Published on the Internet* **65**, 1–216203 (2021).

68. M. Fouquin, J. Hugot, Back to the Future: International Trade Costs and the Two Globalizations. *CEPII Working Paper* **May**, 3–49 (2016).

69. C. Muir, comtradr: Interface with the United Nations Comtrade API. R package version 0.3.0 (2022).

70. M. J. Mangiante, *et al.*, Trends in nonindigenous aquatic species richness in the United States reveal shifting spatial and temporal patterns of species introductions. *Aquatic Invasions* **13**, 323–338 (2018).

71. R Core Team, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria (2022) (July 28, 2022).

414 **Figures**
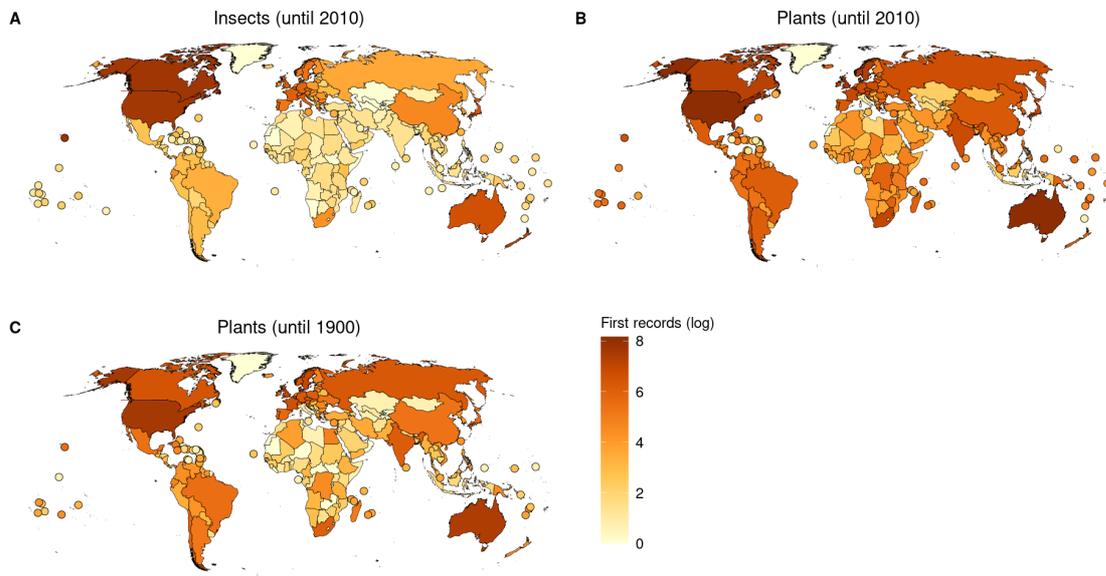
Figure 1: Number of first records (log-transformed) of non-native insects (A) and plants (B & C)
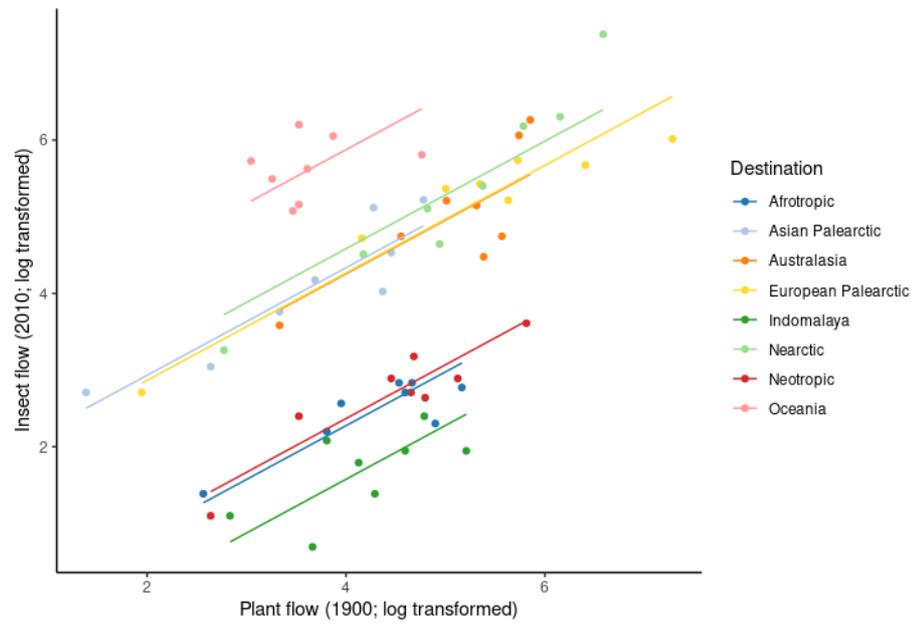per country.

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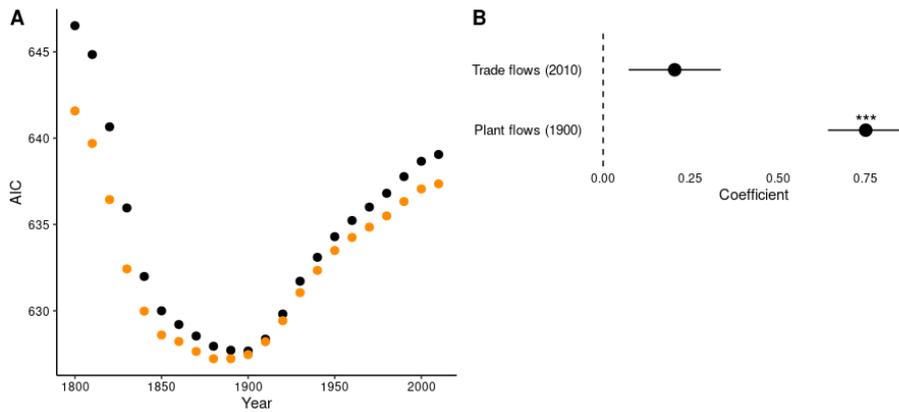
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Figure 2: A) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) as a predictor (black) and including general trade flows of 2010 as a second predictor (orange). AIC values were averaged using a 30-year sliding window for visualisation. B) Estimates of trade flows (2010) and non-native plant flows (1900) as predictors for current (2010) non-native insect flows in GLMM. Explanatory variables were standardized to a mean of 0 and a variance of 1 to allow coefficient comparison.

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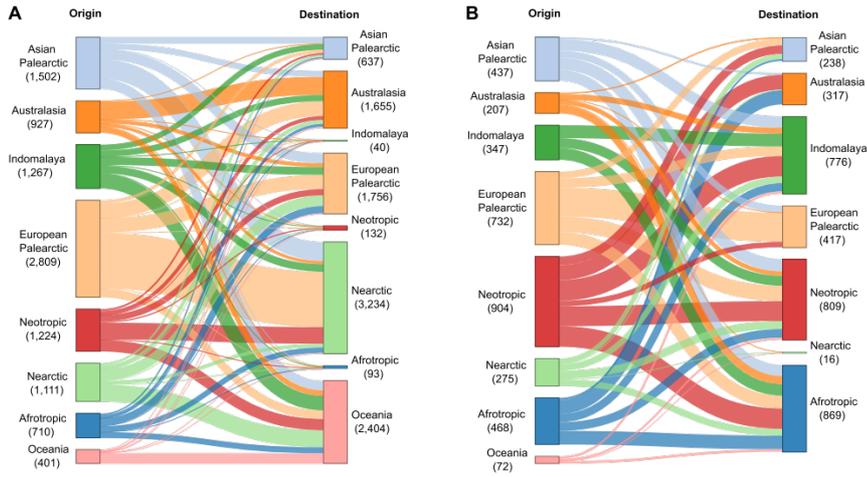
432 **Figure 3:** Observed flows of non-native insects through 2010 (A) and estimated insect invasion
433   debt (B). The number of species is given in parenthesis for each origin and recipient region.
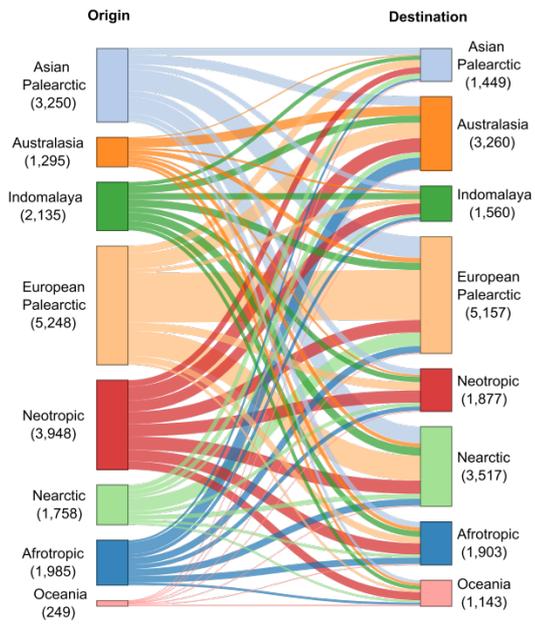434
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437 **Supplementary information**
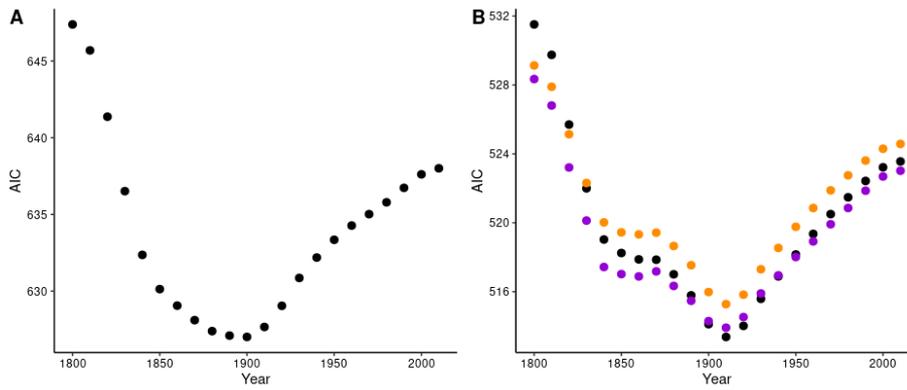
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442 **Supplementary figure 1:** Correlation between insect flows (2010) and plant flows (1900)
443 including the destination of the flow as random effect on the intercept.

Origin — Destination

Asian Palearctic (3,250), Australasia (1,295), Indomalaya (2,135), European Palearctic (5,248), Neotropic (3,948), Nearctic (1,758), Afrotropic (1,985), Oceania (249)

Asian Palearctic (1,449), Australasia (3,260), Indomalaya (1,560), European Palearctic (5,157), Neotropic (1,877), Nearctic (3,517), Afrotropic (1,903), Oceania (1,143)

444   **Supplementary figure 2:** Observed flows of non-native plants through 2010
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Supplementary figure 3: A) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) and sampling effort as predictors. B) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) as a predictor (black), and including general trade flows of 1900 (purple) and 2010 (orange) as a second predictor. To allow comparison between the three model groups, the number of flows in all the models was restricted to pairs of origin-destination regions for which trade flow data were available for both 1900 and 2010. (A, B) AIC values were averaged using a 30-year sliding window for visualisation.

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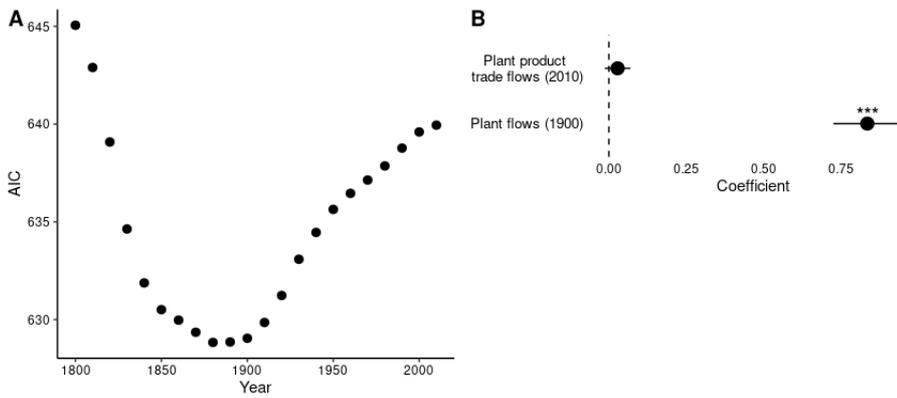
Supplementary figure 4: A) Fit of the GLMMs of current non-native insect flows between each region as a function of non-native plant flows (based on cumulative values up to the year shown on the x axis) and plant product trade flows of 2010 as predictors. AIC values were averaged using a 30-year sliding window for visualisation. B) Estimates of plant product trade flows (2010) and non-native plant flows (1900) as predictors for current (2010) non-native insect flows in GLMM model. Explanatory variables were standardized to a mean of 0 and a variance of 1 to allow coefficient comparison.

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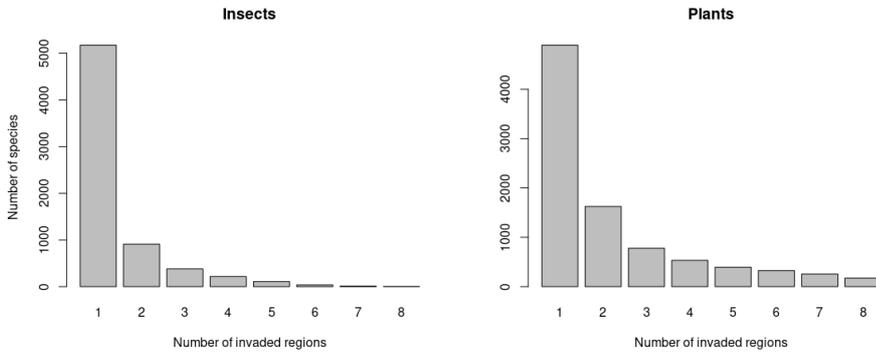
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471 **Supplementary figure 5:** Number of non-native insect and plant species recorded in one to eight
472 biogeographic regions. 76% of the non-native insect species were recorded in only 1 region, 54%
473 for the plants.
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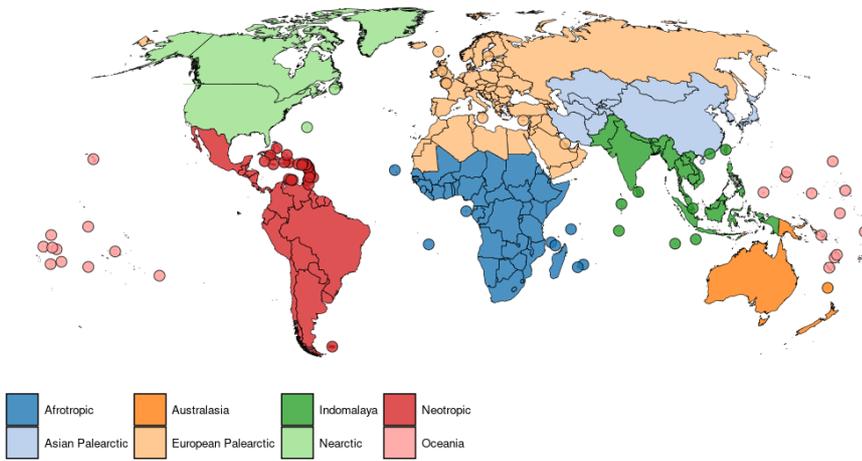
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480 **Supplementary figure 6:** Biogeographic regions

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483 **Supplementary materials and methods**
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485 <u>Sampling effort proxy:</u>
486 We used the number of native insect occurrences per square kilometer as a proxy for sampling effort
487 for each biogeographic region. We extracted insect occurrences from GBIF (1). We removed the
488 occurrences of non-native insect species to consider only native insect occurrences. As some areas
489 are highly unsuitable for insects, they could bias our proxy for sampling effort as these areas contain
490 very few insect occurrences, but not because of a lack of observation but rather because very few
491 insect species live there. To address this bias, we excluded the highly unsuitable areas to compute the
492 proxy for sampling effort. We used the Köppen-Geiger climate classification (2) at 0.5° resolution
493 and excluded the areas falling in BWh (Arid, desert, hot), BWk (Arid, desert, cold), ET (Polar, tundra)
494 and EF (Polar, frost) climate categories. For each region, sampling effort was then computed as the
495 number of native insect occurrences divided by the size of the region, excluding the unsuitable part
496 of it.
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498

1. GBIF.org, GBIF Insect Occurrence Download (2021)
    https:/doi.org/https://doi.org/10.15468/dl.8bw6hc (July 28, 2022).

2. H. E. Beck, *et al.*, Present and future köppen-geiger climate classification maps at 1-km
    resolution. *Scientific Data* **5**, 1–12 (2018).

499