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Historical plant introductions predict current insect invasions

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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, nonnative plants provide habitat and resources for invading insects, thereby facilitating their establishment. Furthermore, plant imports represent one of the main pathways for accidental nonnative insect introductions. Here, we tested the hypothesis that plant invasions precede and promote insect invasions. We found that geographical variation in current nonnative insect flows was best explained by nonnative plant flows dating back to 1900 rather than by more recent plant flows. Interestingly, nonnative plant flows were a better predictor of insect invasions than potentially confounding socioeconomic 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 nonnative insect species. Overall, our results highlight the strong link between plant and insect invasions and show that limiting the spread of nonnative plants might be key to preventing future invasions of both plants and insects.

nonnative insects | nonnative plants | time lag | invasion debt | species flow

Significance

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 nonnative 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 nonnative 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 nonnative plants will be key to preventing future insect invasions.

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 nonnative species are called invasive, either because they have very good spread capacities or because they strongly impact ecosystems and human societies (1). With now more than 7,000 species established outside of their native range, insects outnumber all other nonnative 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). Nonnative 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 nonnative 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 nonnative 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). Nonnative plant diversity is also an important driver of insect invasions (21) as they can facilitate the establishment and spread of nonnative insect species, in particular those that rely on plants as hosts (22–25). Nonnative plants can also promote invasions of

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pollinators and plant visitors (26, 27). While it has been shown that areas with higher numbers of native and nonnative plant species also harbor higher numbers of invasive insects (21), it remains unknown whether 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 nonnative species establishment have been previously identified. For many taxa, the current distribution of nonnative species is better explained by socioeconomic 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 socioeconomic activities lead to an "invasion debt" (28), caused by past socioeconomic 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 the introduction of species by future trade activities. Here, we tested the predictive power of lagged vs. current nonnative plant flows (from years 1800 to 2010) for nonnative insect invasions at a global scale. We not only focused on species classified as invasive, but included all nonnative insect and plant species in our analysis. We built generalized linear models of nonnative insect flows between biogeographic regions, using data of nonnative plant and insect first record dates per region and information on their native range. As global trade dynamics strongly influence biological invasions (30–32), we also included lagged and current trade flows in the models. In this analysis, we i) tested the predictive power of lagged vs. current nonnative plant flows and confounding variables on insect invasions, ii) quantified the time lag between plant and insect invasions, and iii) estimated insect invasion debt in each biogeographic 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 (Fig. 1*A*). In comparison, records of nonnative insect species are much more limited in the Asian Palearctic, the Neotropics, the Afrotropics, and Indomalaya. But nonnative insect richness in these regions is likely to be largely underestimated as these regions are undersampled (33). Similar invasion patterns were observed for plants through 1900, with Europe, the Nearctic, and Australasia being the main recipients of historical plant introductions (Fig. 1*C*). Since 1900, many nonnative plant species have been recorded in the Afrotropics, Oceania, and Asia (Fig. 1*B*). The current distribution of nonnative insects is therefore more correlated to the distribution of nonnative plants from 1900 (linear model R^2 = 0.57) rather than 2010 (linear model R^2 = 0.48).

Time Lag between Plant and Insect Invasions. We used generalized linear mixed models (GLMMs) to test the predictive power of historical and current nonnative plant flows on nonnative insect flows between biogeographic regions. We found that current nonnative insect flows were best explained by nonnative plant flows up to 1900, as indicated by the lowest AIC [AIC = 627.5; Nakagawa's R^2 = 0.95 (34), Fig. 2*A*], rather than by more recent plant flows. The relationship between plant and insect flows is shown in *SI Appendix*, Fig. S1. 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 (*SI Appendix*, Fig. S3*A*). We then tested for the

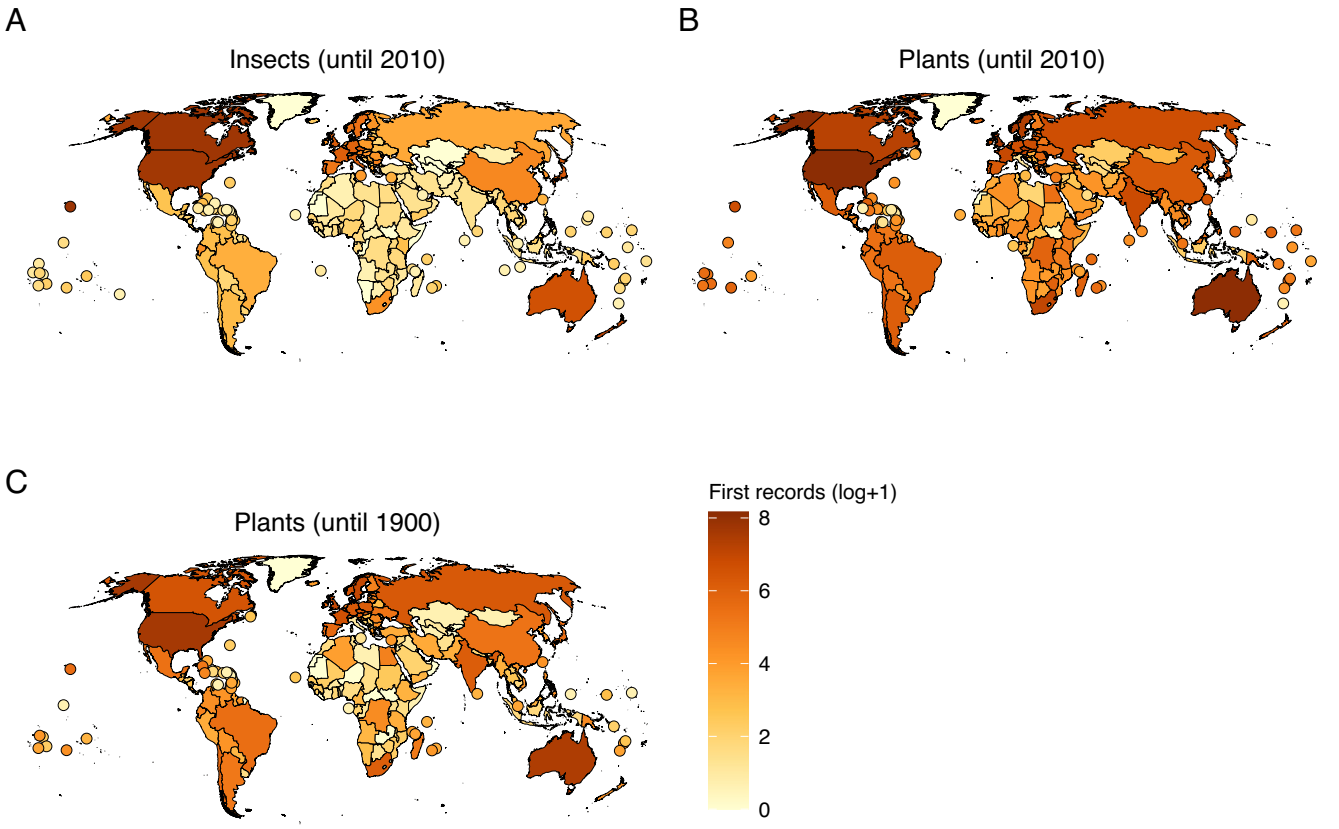

Fig. 1. Number of first records (log-transformed) of nonnative insects (*A*) and plants (*B* and *C*) per country.

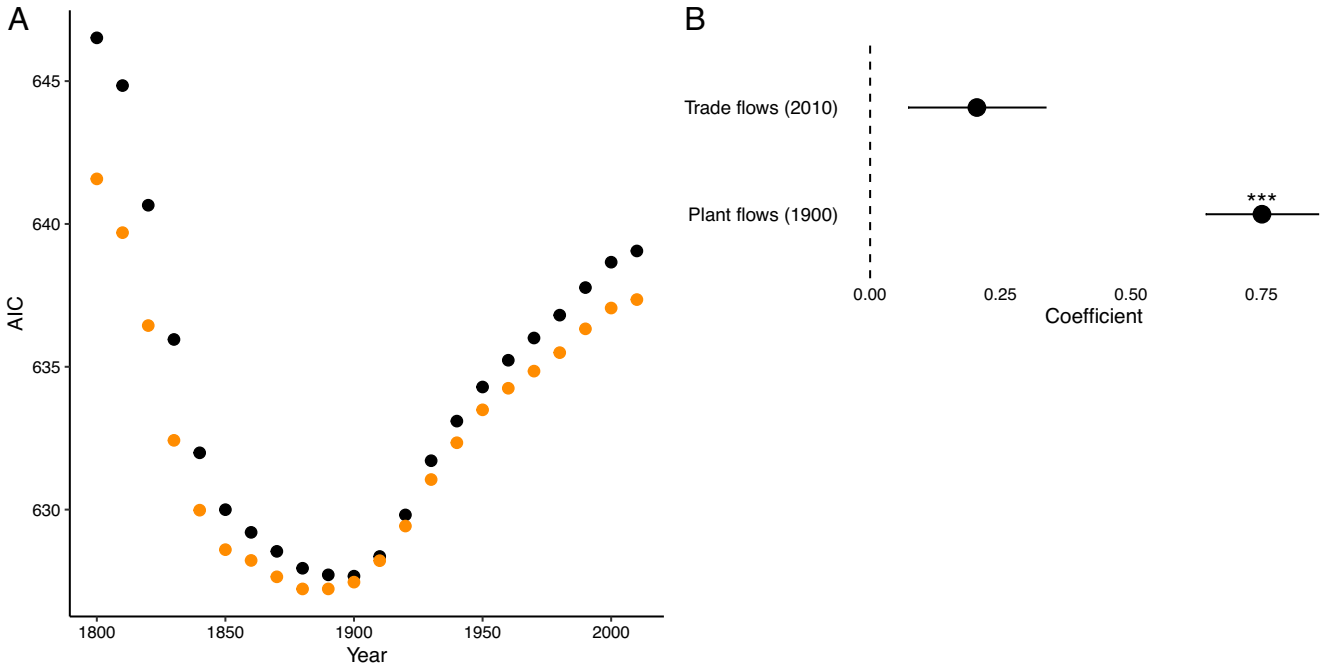

Fig. 2. (*A*) Fit of the GLMMs of current nonnative insect flows between each region as a function of nonnative plant flows (based on cumulative values up to the year shown on the *x* axis) as a predictor (black) and including general trade flows of 2010 as a second predictor (orange). AIC values were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

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 (Fig. 2*A* and *SI Appendix*, Figs. S3*B* and S4*A*). Finally, nonnative plant flows were a better predictor of nonnative insect invasions than general trade flows and plant product trade flows (Fig. 2*B* and *SI Appendix*, Fig. S4*B*).

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 nonnative plant flows of 1900) to predict the expected nonnative insects flows between regions given the total flows of plants observed until 2010. We then computed the insect invasion debt as the difference between the expected flows of nonnative insects and the observed flows (Fig. 3*B*). We found a global debt of 3,442 insect introductions across all biogeographic regions (Fig. 3*B*). So far, a total of 9,952 insect introductions (7,592 species) have been recorded from the eight regions (Fig. 3*A*). 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 nonnative insects have currently been recorded in these regions. Our results suggest that the number of nonnative 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 (Fig. 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 nonnative insect species. The debt was relatively high in the European Palearctic (417 species) and Australasia (317 species) despite the fact that many nonnative insects have already been introduced in these regions (Fig. 3). Finally, the Neotropics are expected to be the greatest source of insect invasions in the future (904 exported species), followed by the European Palearctic (732 species, Fig. 3*B*).

Discussion

Current interregional nonnative insect flows are best explained by nonnative plant flows through 1900 compared to more recent plant flows, indicating that plant introductions precede invasions of nonnative insect species that use these plants as host (24, 25, 36). There are several potential explanations for the extensive time lag. First, nonnative host plants must increase in abundance and start spreading, which can be protracted, before nonnative insects are able to establish and spread in turn. 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. Since only some, but not all, plants are transporting insects, a high number of plant introduction events may be necessary before an insect species can establish, which might also contribute to the extensive time lag. Furthermore, our analyses included all nonnative 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, following the establishment of herbivores and pollinators, invasions of predators and parasitoids may be indirectly facilitated. 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 y for plant-feeding Hemiptera which are small and easily overlooked. This suggests

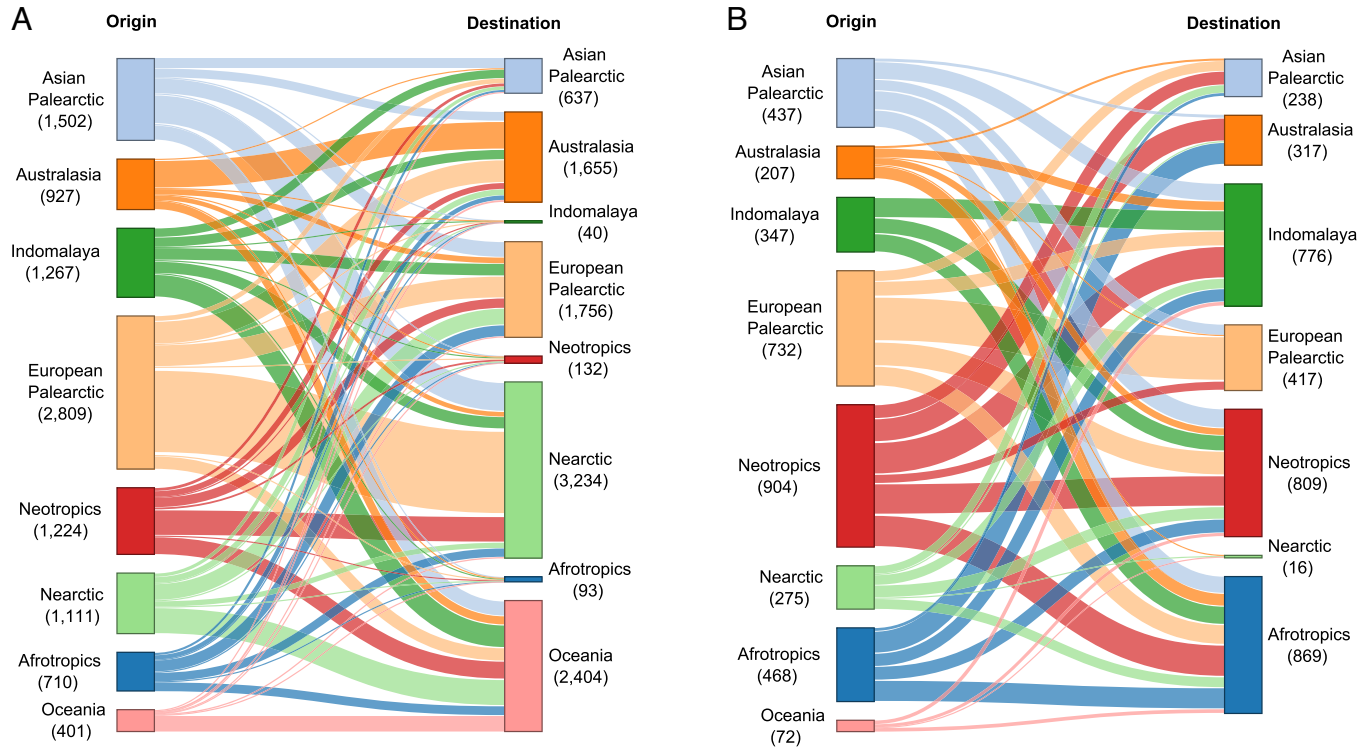

Fig. 3. Observed flows of nonnative insects through 2010 (*A*) and estimated insect invasion debt (*B*). The number of species is given in parenthesis for each origin and recipient region.

that the actual time lag between plant and insect establishment may be shorter than we observed. Nonnative 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. 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 nonnative 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 nonnative 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, but other factors such as biosecurity measures and national policies on imports also influence insect invasions. Moreover, we assume that the slope of the relationship between plant and insect invasions is constant over time. Our analysis therefore provides an assessment of insect invasion debt per region, but further research is required to precisely estimate invasion risk as well as the insect taxa most likely to be introduced in the different regions.

Although a high number of insects have already established in the European Palearctic and Australasia, we found an important debt in these regions. Most future insect introductions in the European Palearctic are expected to be intracontinental, which is consistent with the many intracontinental plant introductions observed in this region (*SI Appendix*, Fig. S2) (48). The debt for Oceania was null, and very small for the Nearctic, as many insects have already established and have been recorded in these regions. But this does not indicate that insect species will no longer be introduced in these regions, since importations of commodities and the introduction of new nonnative plants in the future are likely to promote new insect invasions, if the potential source pool of emergent nonnative species is not depleted. Previous research has indicated that this should not be the case for nonnative insects in North America (47), while plant invasions may saturate in this region (47), suggesting that, beyond the estimated invasion debt, many new nonnative insects may fail to establish.

Many insects from the European Palearctic have been introduced to the Nearctic. In comparison, fewer insects have been introduced in the opposite direction. Mattson et al. (49) argued that there may be fewer niches for invasive insects in Europe due to the lower host plant diversity in this region caused by the Pleistocene/Holocene glaciations. Although this hypothesis is still

in dispute (20), it could explain this asymmetry in insect invasions. However, a similar asymmetry can be observed for nonnative plants (*SI Appendix*, Fig. S2), with more introductions from the European Palearctic to the Nearctic than in the opposite direction, possibly due to European colonialism (29). Our results therefore suggest that the asymmetry in insect invasions might be driven by the asymmetry in plant invasions.

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

A potential limitation of our approach is that it does not account for "bridgehead effects." The bridgehead effect is a phenomenon of secondary spread where nonnative insects arrive to a new region from a previously invaded region, rather than directly from the native range (50). This phenomenon has a strong impact on the spread of nonnative insects (50–53). If a high proportion of species are established in several continents, bridgehead effects tend to be more frequent which can distort our global view of nonnative species flows (54). But in this analysis, the majority of nonnative insect and plant species were recorded in only one biogeographic region (*SI Appendix*, Fig. S5), which suggests that recorded nonnative species flows largely reflect actual introduction routes. Moreover, it appears that insects follow similar invasion patterns as the plants with which they have coevolved within their native range, regardless if they were introduced directly from their native range or from a bridgehead region. Our aim was not to predict the exact future spread routes, but rather to anticipate future flows of nonnative insects from donor to recipient regions.

Our analysis revealed an important time lag between plant and insect invasions at a global scale. Further research could investigate this time lag at the scale of individual insect species for which the host plant species are known. Our data did not include georeferenced records and therefore we cannot confirm that nonnative insects and plants are actually co-occurring, but previous studies suggest that it is very likely to be the case (25–27). Future studies might also assess the effect of nonnative plants which have been planted for agriculture, forestry, or horticulture but have not managed to establish populations in the wild yet. These species are not represented in our data, but may also contribute to the spread of nonnative insects specializing on those plants (24, 55). Similarly, many invasive insects may be associated with ornamental plants used in urban landscapes (56).

Time lags between plant and insect invasions may vary among taxonomic groups, feeding guilds, and also among regions. Understanding what drives these time lags would inform efforts to better predict and manage future insect invasions. Future research could also investigate the effect of nonnative plant abundance, rather than just species richness, on nonnative insect establishment. It is likely that the probability of insect establishment increases as nonnative plants spread and increase in abundance in a given region.

Overall, we have shown that global insect invasions lag behind plant invasions. Given patterns of recent plant introductions, insect invasions are expected to rise in tropical regions, which could strongly impact local economies and threaten biodiversity. Our study highlights that nonnative plants can have indirect environmental consequences by facilitating insect invasions. Including the risk of insect introduction in invasion risk screening tools might therefore be necessary when assessing the potential impact of nonnative plants. Targeting plant imports (57) and limiting the establishment and spread of nonnative plants might also help to reduce invasions of insect in the future.

Materials and Methods

Nonnative Species Flows. Records of insect establishments and plant naturalizations were compiled for each of the eight world biogeographic regions (Asian Palearctic, European Palearctic, Afrotropics, Neotropics, Indomalaya, Nearctic, Australasia, and Oceania) using a system modified from Wallace's designation and snapped to country borders (*SI Appendix*, Fig. S6). We extracted data of nonnative 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 nonnative 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 nonnative 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 nonnative 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 nonnative insect species and 54,020 naturalization records of 10,560 nonnative plant species made prior to 2010. We did not include data from the most recent years (2011 to present) as they are incomplete because of the delay in the publication of new nonnative 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 nonnative 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 nonnative insect and 85% of nonnative plant species. We then used the nonnative species first records per biogeographic region and their native ranges to reconstruct flows of nonnative 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 (http://www.cepii.fr/CEPII/en/bdd_modele/bdd_modele_item.asp?id=32). 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* (68). 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 nonnative plant flows on nonnative 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 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, but we tested the correlation between the number of insect and plant species that were moved from a donor to a recipient 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 nonnative plant flows until the 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 nonnative

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 nonnative plants have been recorded before that date (2). This resulted in 22 GLMMs predicting current insect flows as a function of plant flows cutoff at each decade (from 1800 to 2010). We also included origin and destination of the nonnative 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 summarized as:

Insect flows (through 2010) ~ Plant flows (through year x) + (1|origin) + (1|destination)

To test for the predictive power of lagged and current trade flows on nonnative 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, 69). 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 (*SI Appendix, Materials and Methods*).

Estimating Insect Invasion Debt. We used the coefficient of the best model (i.e., with nonnative plant flows until the year 1900, Fig. 2*A*) to predict the expected flows of nonnative insects given the total flows of nonnative plants observed until 2010. We then subtracted the current nonnative insect flow (i.e., the total flow of nonnative insect species discovered up to 2010) from the predicted flow of nonnative insects, and thereby obtained the insect invasion debt. We therefore used a single predictor, current nonnative plant flows, to estimate the insect invasion debt. We also assume that the slope of the relationship between plant and insect flows is constant over time.

All analyses were performed with R 4.1.2. (70).

Data, Materials, and Software Availability. Previously published data were used for this work (2, 46, 59–63, 67). Code used to perform analysis and generate figures is available at: https://doi.org/10.5281/zenodo.7945261 (71).

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