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RESEARCH ARTICLE

The world's 100 worst invasive alien insect species differ in their characteristics from related non-invasive species

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Handling Editor: Martín Nuñez**Abstract**

1. While there has been great interest in species characteristics that promote invasiveness, still little is known about the characteristics that distinguish invasive from non-invasive insects. Using a database on the naturalised distributions of alien insects and expert opinions about their impacts, we identified the world's 100 worst invasive insect species.
2. By comparing species characteristics reported in the literature using a meta-analysis, between the 100 worst invasive species and related non-invasive species, we found that invasive insects overall have more pathways of introduction, occur in more habitats, have higher fecundities, higher voltinism, more genes, shorter lifespans and faster development from egg to adult. Some of the differences in species characteristics related to propagule pressures, life-histories and biotic interactions, conditional on whether the non-invasive species compared is known to be naturalised somewhere, whether the invasive species is globally distributed, and the climatic region of the species.
3. *Synthesis and applications.* We show for the first time, using a multi-species comparative approach, that invasive insects differ in several characteristics from related non-invasive insects. Our results show that invasive species, such as *Spodoptera frugiperda*, typically are habitat generalists with a high fecundity, a short lifespan and fast development, whereas the importance of female body size and number of enemies are context dependent. Our study can guide and improve existing screening tools for assessing the invasion potential of alien insects.

KEYWORDS

fecundity, introduction pathway, invasion syndromes, invasiveness, life history, lifespan, non-native species

1 | INTRODUCTION

Owing to globalisation and the resulting breakdown of biogeographic barriers, alien organisms have in the last century been introduced into new regions at an unprecedented rate (Ricciardi, 2007; Seebens et al., 2018). Some of those aliens have been successfully naturalised in the new ranges (i.e. have established self-sustaining populations in the wild), and some of those have become invasive (i.e. have spread rapidly; Blackburn et al., 2011), frequently causing environmental or socioeconomic damage (CBD, 2000). Among the large number of insects that have become naturalised, many are invasive pests in agriculture or forestry, or are vectors of diseases (Bonnamour et al., 2021; Ricciardi, 2007). What drives the invasiveness of insects, however, remains largely unknown.

Studies in invasion science have been focusing on identifying invasion characteristics (i.e. pathways, life-history traits and characteristics of the recipient ecosystems; Novoa et al., 2020), with the goal of predicting potential future invasive alien species (Catford et al., 2022; Labrie et al., 2006). So far, most studies comparing invasive to non-invasive species have focused on vascular plants and vertebrates (Jelbert et al., 2019). This has revealed that the invasiveness of alien plants is frequently related to introduction effort (e.g. Dehnen-Schmutz et al., 2007) and species traits such as size, growth rate, lifespan and reproduction (van Kleunen et al., 2010). The invasiveness of mammals is also frequently related to introduction effort (Courchamp et al., 2003) and to lifespan and body mass (Capellini et al., 2015). For insects, less data is available. Consequently, although some invasive insect pests, such as the whitefly (*Bemisia tabaci*), the red imported fire ant (*Solenopsis invicta*) and the Mediterranean fruit fly (*Ceratitidis capitata*), have been intensively studied, how they differ from non-invasive insects remains largely unexplored (Bates et al., 2020; Fournier et al., 2019).

Synthesis research has become increasingly important in the fields of ecology and evolution because it helps to comprehensively summarise the available evidence in a transparent and objective manner (Gurevitch et al., 2018). For example, a meta-analysis on the results of 117 studies, comparing life-history traits between 125 invasive and 196 non-invasive plant species, showed that the invasive ones generally have higher trait values (van Kleunen et al., 2010). Such meta-analyses and other comparative analyses can be used to develop statistical models to predict invasiveness with reasonable accuracy (Nunez-Mir et al., 2019). Whether species characteristics related to invasiveness, as identified for plants and other groups of organisms, such as high fecundity, strong plasticity and long lifespan (Palma et al., 2021), also apply to insects remains unknown (Gray et al., 2009). Our current knowledge is still often inconclusive due to limitations in experimental data and/or the scope of potential invasion traits analysed (Brockerhoff & Liebhold, 2017).

Here, we use a global database on naturalised alien insects in combination with expert judgement to identify the world's 100 worst invasive alien insect species. We then explored whether these invasive insect species differ from related non-invasive insect species regarding the numbers of introduction pathways and

habitats, life-history and genomic traits, and the number of enemies. The results of this study can guide and improve existing screening tools for assessing the invasion potential of alien insects (Gippet & Bertelsmeier, 2021; Leffler et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Identifying the world's 100 worst invasive alien insect species

We compiled a list of the world's 100 worst invasive alien insects in a two-step process. In the first step, we used the most comprehensive global inventory of alien insects available to identify the 150 most widespread alien insect species. This inventory was compiled from multiple data sources, including the Global Invasive Species Database (<http://www.iucngisd.org/gisd/>); Invasive Species Specialist Group of the IUCN Species Survival Commission, 2021), the Centre for Agriculture and Bioscience International (<https://www.cabi.org/>); CABI, 2021) and the Global Register of Introduced and Invasive Species (<https://griis.org/>); Pagad et al., 2018). We also searched for inventories of alien insect species worldwide and integrated data on occurrences and geographical distributions, including lists of alien insects published in scientific journals. This inventory includes a total of 7741 alien insect species (Appendix S1) covering all countries worldwide. The database also includes information on the insect order that the species belongs to, and, if available, information on the native continent(s) and climatic region of the species. We selected the 150 species that have invaded the largest number of countries.

In a second step, these 150 species were evaluated with regard to their impacts on the environment, economy and human health. We did this by calculating impact scores based on a questionnaire survey (see Table S1). The impact score had three categories: strong impact (1), mild impact (0) and no significant impact (-1). We received 31 complete evaluations. The participants were free to withdraw from the questionnaire during our survey. Then, the 50 species with the lowest average impact scores were removed from our list. The remaining 100 species, that is those with large alien distributions and strong impacts, were considered the world's worst invasive insect species (<https://doi.org/10.5061/dryad.xksn02vmv>) and were used in our analyses.

To determine the research status of the invasive alien insects, we also extracted information on the numbers of publications for each of them by searching the Web of Science Core Collection (accessed on 14 February 2022) for the respective scientific names of the species. For example, a search for "*Apis mellifera*" yielded 33,842 publications.

2.2 | Selection of species characteristics potentially related to invasiveness

For each of the 100 invasive alien species, we searched for data on 10 species characteristics that might be related to invasiveness

(Brockerhoff & Liebhold, 2017; Tayeh et al., 2015): the number of introduction pathways, the number of habitats it occurs in, five life-history traits, the number of enemies and two genomic traits. We also searched for such data for non-invasive species that are phylogenetically closely related to the invasive alien species (i.e. species in the same genus or family). This allowed us to do a comparative analysis by calculating mean effect sizes for each pair of invasive and non-invasive species (Levin et al., 2020). For comparison of genomic traits, the available data was very unbalanced among taxa. For example, species in the genera *Drosophila* and *Apis* had more genomic information than any other genus. To enlarge the number of data points for comparisons of genomic traits, we used all possible species pairs, even if some of these pairs included the same invasive species.

The 10 variables were classified into five categories, based on the invasion process (Catford et al., 2022; Novoa et al., 2020). The first category is related to the movement of propagules, which includes one variable: the number of introduction pathways (with the categories release, escape, contaminant, stowaway and unaided; Hulme et al., 2008). The second category is related to whether the species is a habitat specialist or generalist: the number of habitats the species occurs in (with the categories agriculture, forest, grassland, urban area and indoors [in the houses]). The third category consists of five life-history traits: female body size, adult lifespan, the growth degree-days from egg to adult (i.e. effective accumulated temperature, EAT), fecundity capacity (average number of eggs laid per female during the whole life time), and voltinism (number of generations per year). The fourth category is related to biotic interactions and includes one variable: the species' number of enemies. The fifth category covers genomic information and includes two variables: genome size (Mb) and the number of identified genes.

For all pairs of invasive and non-invasive insect species, we collected all available data on the 10 variables from published papers, book chapters, publicly accessible online databases and academic theses. All genomic information was downloaded from the website of the NCBI (National Center for Biotechnology Information, 2021).

2.3 | Effect sizes

We used the log response ratio (RR) as effect size because it is the most widely used effect-size metric in ecological and evolutionary meta-analyses (Bakbergenuly et al., 2020; Lajeunesse, 2015). RR has preferable statistical properties over other effect-size metrics as it is not biased by differences in sample sizes and usually follows a Gaussian distribution (Hedges et al., 1999). We calculated RR and its 95% confidence interval (CI) for the difference between the invasive and non-invasive species in each pair for each of the 10 variables by using the following equations:

$$RR = \ln\left(\frac{\bar{X}_I}{\bar{X}_N}\right) \text{ and } CI = Z_{\alpha/2} \cdot \sqrt{\frac{s_I^2}{n_I \bar{X}_I^2} + \frac{s_N^2}{n_N \bar{X}_N^2}},$$

where \bar{X}_I and \bar{X}_N are the mean values of the species characteristic for the invasive and non-invasive species within a pair, respectively; s_I^2 and s_N^2 their standard deviations; n_I and n_N their sample sizes; $Z_{\alpha/2}$ is the confidence interval critical value for level α ($= 0.05$). Negative values of RR indicate lower values for invasive than for non-invasive species, and positive values indicate the opposite. The mean RR values were calculated over all species pairs, and the 95% CI was estimated based on bootstrapping (resampling 1000 times with replacement), which avoids pseudo-replication caused by paired comparisons of small sample sizes (de Almeida-Rocha et al., 2017). The bootstrap method further improves the reliability of evidence synthesis by increasing the sample size.

We also assessed whether the non-invasive control species is known to be a naturalised alien somewhere in the world (but not invasive) based on our naturalised insect database. Furthermore, we extracted information from the naturalised insect database on whether the invasive alien species is originally from a temperate climate or from a subtropical to tropical climate, and whether the invasive species is globally distributed (on six continents, irrespective of whether it is native or alien there) or not (fewer than 6 continents). For the sub-group analysis, we removed the species pairs with no or uncertain records of geographical distribution and climate origins.

The mean effect sizes were calculated using the 'rma' function of the 'metafor' package, which is based on linear mixed models with the restricted maximum-likelihood method in the R statistical software (R Core Team, 2020; Viechtbauer, 2010). This approach is an approximately unbiased and efficient way for examining whether the mean effect size differs significantly from zero. We followed the standard calculation based on statistical inference of the mean values and their 95% CIs, rather than on significance tests (Nakagawa et al., 2022). If the 95% CI does not overlap with zero, this indicates a significant difference between invasive and non-invasive species. For visualisation of the effect size, we used the following equation to translate the RR values and 95% CIs into percentage changes:

$$P = (e^{RR} - 1) \times 100\%.$$

2.4 | Effect-size heterogeneity tests

For each of the 10 species characteristics, we tested for heterogeneity in effect sizes and whether this heterogeneity could be contributed to different explanatory variables. Heterogeneity of effect sizes was assessed with the classic method of the Q-test (QT) using the 'metacont' function (Schwarzer et al., 2015). A high QT means that the variance in the mean effect sizes among species pairs is significantly greater than expected, indicating that certain factors might explain part of this variance. As possible explanatory factors, we used whether or not the non-invasive control species is known to be naturalised somewhere in the world, whether the invasive species is globally distributed (i.e. on all 6 continents or fewer), and whether it has a temperate or (sub) tropical origin. Each of these explanatory factors was tested separately as a categorical moderator in a mixed-effect meta-regression model. We only present the results for the variables for which we had at least seven species pairs, because fewer data will lead to unreliable results.

All calculations were performed with the 'metafor', 'meta' and 'bootstrap' packages in R version 4.1 (R Core Team, 2020) using the R Studio 1.4.1717 interface. All graphs were generated by using Origin Pro 2021 (Origin Lab, 2021).

3 | RESULTS

3.1 | Basic information of the world's 100 worst invasive alien insects

The world's 100 worst invasive insect species are taxonomically very diverse (Figure 1a) and include representatives of five of the largest insect orders, including Hemiptera (25 species), Coleoptera (23), Lepidoptera (18), Hymenoptera (15) and Diptera (12). Most of the 100 invasive species occur in agricultural habitats (32%), followed by forests (23%) and urban habitats (21%) (Figure 1b). The indoor environment (11%) also harbours some seriously invasive species damaging human health or contaminating food (e.g. *Aedes aegypti* and *Ae. albopictus*; Figure 1b). The most common pathway of introduction is contaminant (39%), followed by unaided (28%) and stowaway (25%; Figure 1c).

Asia is the largest donor of invasive alien insects, with 34 species, followed by North America (23), and the smallest donor (not considering Antarctica) is Oceania (7) (Figure 1d). Furthermore, Europe is the largest recipient of invasive aliens, with 83 species, followed by North America (64) and Africa (63) (Figure 1e). The continent with the largest species exchange (i.e. the sum of the numbers of received and donated species) was Europe, followed by North America and Asia (Figure 1f). The crazy ant (*Paratrechina longicornis*), originating from tropical Africa, is the most widely distributed alien species as it has invaded more than 130 countries. The most widely studied invasive species is the western honeybee (*Apis mellifera*), with 33,842 publications, followed by the yellow fever mosquito (*Ae. aegypti*, 29,405 publications) and the Asian tiger mosquito (*Ae. albopictus*, 12,760 publications; Figure 1g). The fall armyworm (*Spodoptera frugiperda*), originating from tropical-subtropical climates in the Americas, is the most widely studied agricultural pest, with 12,750 publications, followed by the tobacco whitefly (*Bemisia tabaci*, 11,114), the green peach aphid (*Myzus persicae*, 10,312) and the red flour beetle (*Tribolium castaneum*, 8030). The top 20 species of the world's 100 worst invasive aliens accounted for more than 76.7% of the publications.

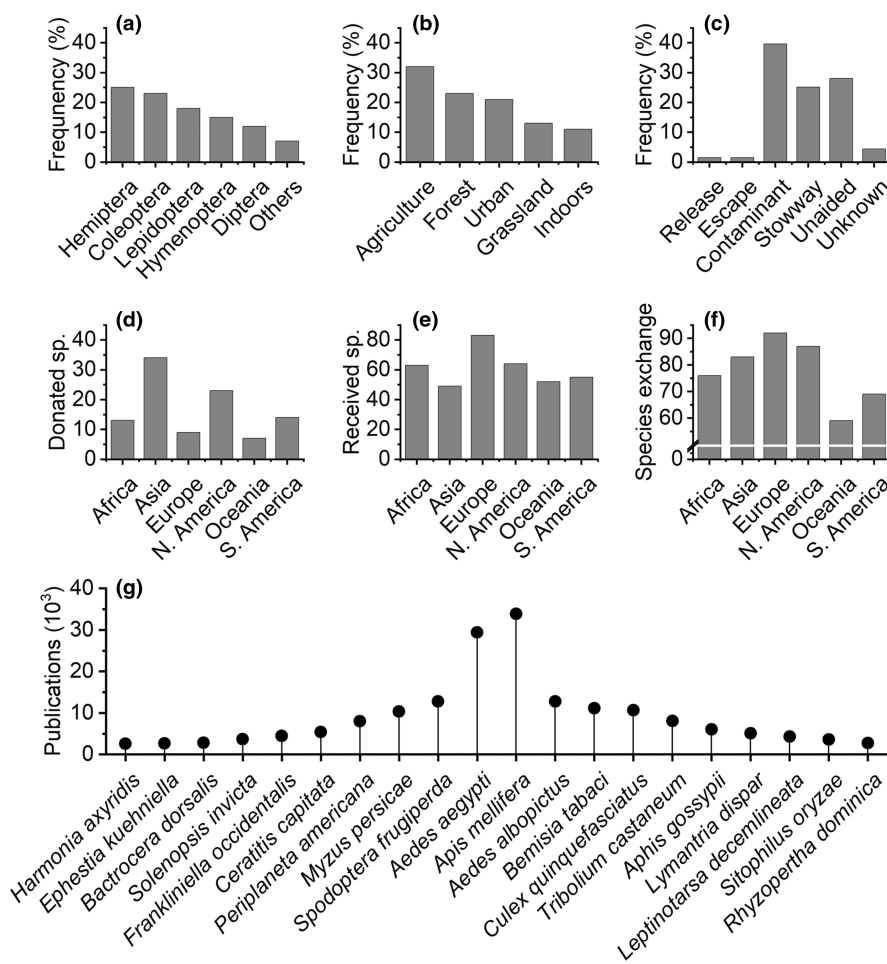


FIGURE 1 Basic statistics of the world's 100 worst invasive alien insects. The percentage frequency of invasive species across (a) insect orders, (b) habitat types and (c) introduction pathways. The invasive species based on (d) the continent of origin and (e) recipient continents. (f) The number of species exchanged (i.e. the received and donated species) per continent. (g) The publications till February 2022 for the 20 most invasive species.

3.2 | Differences between invasive and non-invasive insects

Of the 10 species characteristics included in our analyses (Figures S1–S10), seven differed significantly between invasive and non-invasive insects (Figure 2a). The invasive species have significantly more pathways of introduction to other places ($+24.9 \pm 9.8\%$, see Figure S1a), occur in more habitats ($+34.4 \pm 12.3\%$, see Figure S2a), have a higher fecundity ($31.4 \pm 19.0\%$, see Figure S6a), higher voltinism ($25.1 \pm 14.5\%$, see Figure S7a) and higher values for the number of genes ($+11.8 \pm 8.0\%$, see Figure S10a) but have shorter lifespans ($-16.2 \pm 14.4\%$, see Figure S4a) and require fewer growth degree-days from egg to adult ($-36.4 \pm 20.4\%$, see Figure S5a) than their non-invasive relatives (Figure 2a). Female body size (see Figure S3a), number of enemies (see Figure S8a) and genome size (see Figure S9a) did not significantly differ between invasive and non-invasive insects overall (Figure 2a).

Heterogeneity analysis revealed that the mean effect sizes varied significantly among the different variables ($Q=36.98$, $df=9$, $p<0.001$). For each of the individual variables, however, heterogeneity among the mean effect sizes was not significantly different from the expected sampling errors (all $p>0.1$). Nevertheless, we found that the mean effect sizes depended on some of the moderator factors. For four of the species characteristics, the significance of the effect size depended on whether the non-invasive species compared is known to be naturalised somewhere in the world or not (Figure 3a; Figures S1–S10). When the non-invasive is not known to be naturalised, the invasive species had significantly larger female body sizes and higher voltinism than the non-invasive species, whereas this was not the case when the non-invasive is known to be naturalised somewhere (Figure 3a). On the other hand, when the non-invasive is known to be naturalised, the invasive species had a shorter lifespan and a smaller genome size than the non-invasive species, whereas this was not the case when the non-invasive is not known to be naturalised somewhere (Figure 3a). For both groups, invasive species had significantly more introduction pathways, more habitats they occur in, higher fecundity, more genes and lower EAT than non-invasive species (Figure 3a).

Comparisons of mean effect sizes between species pairs in which the invasive alien is globally distributed (i.e. occurs on all 6 continents) and those that are not (i.e. occur on <6 continents) revealed different patterns for five species characteristics (Figure 3b; Figures S1–S10). When the invasive species are globally distributed, they had significantly shorter life spans and smaller genome sizes than non-invasive species, but these differences were not significant when the invasive species are not globally distributed (Figure 3b). When the invasive species are not globally distributed, they had significantly larger female body sizes, higher voltinism and more genes, but not when they are globally distributed (Figure 3b). For both groups, the invasive species had significantly higher values than the non-invasive ones for the number of introduction pathways, the number of habitats and fecundity (Figure 3b).

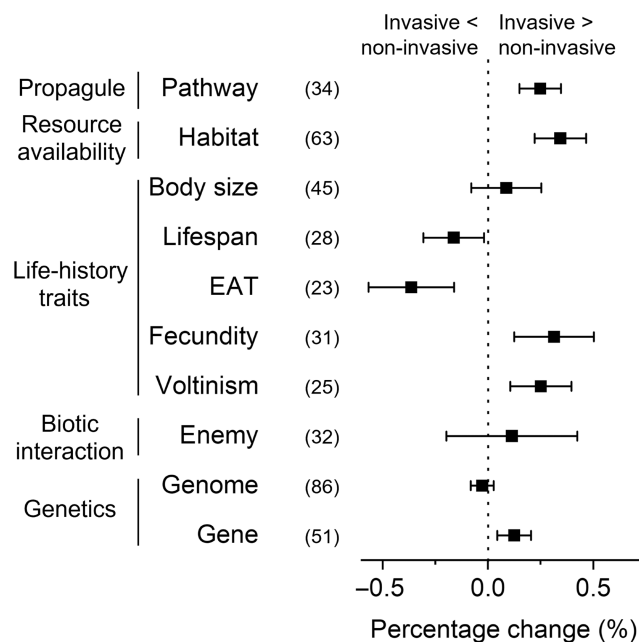


FIGURE 2 Percentage changes and 95% CIs of differences between invasive and non-invasive insects for 10 characteristics (introduction pathways, invaded habitat types, female body size, lifespan, effective accumulated temperature (EAT), fecundity, voltinism, enemies, genome size, genes). The mean effect size of percentage changes (%) is significantly different when the 95% CI does not include zero. The sample sizes of species pairs are given in parentheses.

Comparisons of mean effect sizes between species pairs from sub-tropical to tropical climates and species pairs from temperate climates revealed different patterns for five variables (Figure 3c; Figures S1–S10). For temperate species pairs, invasive species had larger female body sizes and lower EAT than non-invasive species, whereas this was not the case for (sub)tropical species pairs (Figure 3c). Moreover, whereas for (sub)tropical species pairs, invasive species had shorter lifespans and smaller genomes, this was not the case for temperate species (Figure 3c). Furthermore, whereas for temperate species pairs, the invasive species had fewer enemies, the opposite was true for (sub)tropical species pairs (Figure 3c). For both temperate and (sub)tropical species pairs, the invasive species had more introduction pathways, more habitats they occur in, higher fecundity, higher voltinism and more genes than non-invasive species (Figure 3c).

4 | DISCUSSION

Using a database on the naturalised distributions of alien insects and expert opinions about their impacts, we identified the world's 100 worst invasive insect species, with representatives of all major insect orders. We found that invasive insects, compared to non-invasive relatives, have more pathways of introduction, occur in more habitats, have higher fecundities, higher voltinism, more genes, shorter

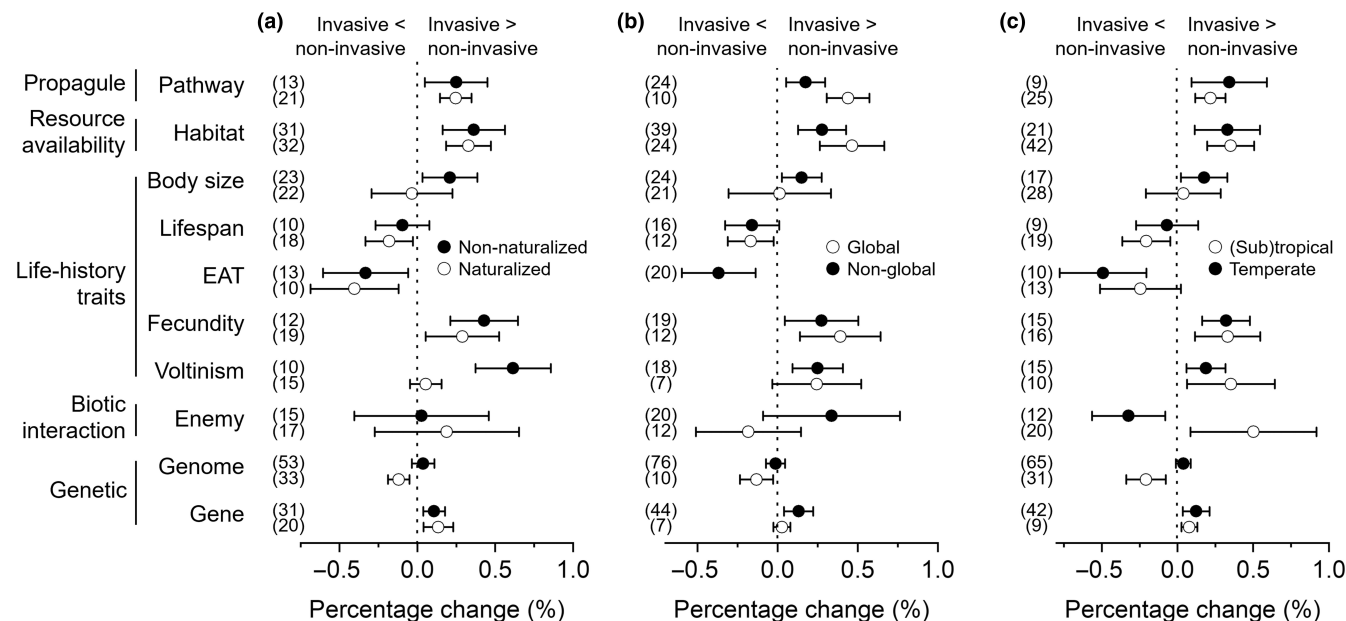


FIGURE 3 Effects of different data groupings on percentage changes and 95% CIs of differences in the species characteristics between invasive and related non-invasive insects. The dependency of percentage changes on (a) whether the non-invasive counterpart species is known to have been naturalised somewhere, (b) whether the invasive species is globally or non-globally distributed and (c) whether the pair of species are from a (sub)tropical or temperate climate. The mean effect size of percentage changes (%) is significantly different between invasive and non-invasive insects when the 95% CI does not include zero. The sample sizes of species pairs are given in parentheses. EAT, effective accumulated temperature.

lifespans and faster development from egg to adult. Some of these differences in species characteristics, related to propagule pressure, life-histories and biotic interactions, are also dependent on whether the non-invasive species compared is known to be naturalised somewhere, whether the invasive species is globally distributed or not, and the climatic region of the species. So, our results show that invasive insects differ from non-invasive ones in species characteristics but that some of those differences are context dependent.

The world's 100 worst species come from all major insect orders, showing that they are taxonomically and phylogenetically diverse. Most of them are pests in agriculture and forestry (Liebhold et al., 2021) but some of them, particularly those that transmit human diseases, can also be found in urban environments and in residential houses (Lounibos, 2002). While some of the invasive species, like the honey bee *Apis mellifera*, do have economic value and were frequently introduced for that reason, most impose negative socio-economic or ecological impacts (Moritz et al., 2005). *Apis mellifera* also has such negative impacts as it may compete for food resources and breeding cavities with native species. Therefore, the established populations of escaped honeybees may lead to further losses of native bee species (Cunningham et al., 2022; Moritz et al., 2005).

Asia and North America are the largest donors, and Europe and North America are the largest recipients of invasive insects. For plants, Asia is also the largest donor of naturalised plants, and Europe and North America are also among the largest recipients (van Kleunen et al., 2015). This could reflect that the same global drivers, such as bilateral trade, are responsible for the introduction of alien species from different taxonomic groups (Banks et al., 2015).

Furthermore, the introduction of many invasive insects that are pests in agriculture and forestry may be tied to the introduction of alien plant material and shipment of wood packaging materials (Brockerhoff & Liebhold, 2017).

It is frequently suggested that propagule pressure, that is the number of introduction events and the number of introduced individuals per event, is a major determinant of invasion success (Lockwood et al., 2005). Although we do not know the actual propagule pressures of alien insects, it is likely that the number of introduction pathways is a good indicator of propagule pressure (Riera et al., 2021). Overall, the number of introduction pathways was higher for invasive than for non-invasive species. The global expansion of invasive species (e.g. the Asian citrus psyllid *Diaphorina citri*) is facilitated through several pathways, suggesting that the introduction of propagules is an important driver of biological invasions (Thomas et al., 2017). Another species characteristic that we found to be consistently higher for invasive than for non-invasive species was the number of habitats a species can inhabit. This supports the idea that habitat generalists are more likely to become invasive than habitat specialists (Crowder & Snyder, 2010). So, our findings support the results of studies on ants (Gippet & Bertelsmeier, 2021) and many other taxonomic groups (Pyšek et al., 2015), showing that proxies of propagule pressures and niche breadth are good predictors of invasiveness.

As invasiveness are closely related to fitness (Stearns, 1992), it is expected that such traits should differ between invasive and non-invasive species (Renault et al., 2018). Indeed, we found significant differences between invasive and non-invasive species for the five

life-history traits for which we had data but some of these differences were context specific. In line with expectations, fecundity capacity was consistently higher for the invasive species than for the non-invasive species, which reflects that a high fecundity is required for fast population growth (Jelbert et al., 2019). As aliens are usually introduced in low propagule sizes, high fecundity can allow the initially small populations to rapidly establish and expand (Gougherty & Davies, 2021).

Overall, invasive species had fast developmental rates from egg to adult, and consequently had more generations per year. This, however, was at the cost of lifespan, suggesting a trade-off between developmental rate and lifespan. Generally, "fast" life histories (i.e. fast developmental rate and short lifespan) are thought to enhance population establishment and expansion by facilitating a faster growth of an invasive population, thereby reducing the period in which the population is small and thus highly vulnerable to extinction. For developmental rate (i.e. EAT), the direction of the difference between invasive and non-invasive insects was relatively consistent, although it was not statistically significant for species of (sub)tropical origin. For voltinism, the direction of the difference was also relatively consistent. However, the difference disappeared when the non-invasive species is known to be naturalised somewhere in the world. This suggests that while naturalised alien species have more generations per year than non-naturalised species (Fahrner & Aukema, 2018), voltinism does not drive invasiveness among naturalised alien insects.

Invasive species also distinguished themselves from other naturalised species in that they overall had shorter lifespans. This may reflect that species with short lifespans usually have rapid development and multivoltinism, which both should facilitate colonisation and dispersal. The effect of female body size on invasiveness, depended strongly on the exact comparison (Kwon & Choi, 2020). Nevertheless, when it did differ, the invasive insects had larger females than their non-invasive relatives. This was the case for species with temperate origins, when the invasive species is globally distributed, or when the non-invasive counterpart is not known to be naturalised anywhere. As a large female body size is frequently linked to a high potential fecundity (Preziosi et al., 1996), this could be one explanation for the association between female body size and invasiveness.

Biotic interactions are thought to play important roles in invasion success of alien species (Crawley, 1987). Interestingly, for species pairs from temperate regions, invasive species had fewer enemies than non-invasive species, but the reverse was true for species pairs from tropical regions. Possibly, this reflects that biotic interactions in temperate regions are more generalised, whereas they are more specialised in tropical regions.

The large-genome constraint hypothesis predicts that plants with small genomes may have higher maximum photosynthetic rates and growth rates (Knight et al., 2005), which could promote invasiveness. Indeed, in plants, invasive species are frequently characterised by having small genomes (Pandit et al., 2014). However, less is known about other taxonomic groups. For insects, we found no overall difference in genome size between invasive and

non-invasive species but when there was a difference—as was the case when the species originated from tropical regions, when the invaders have a global distribution and when their non-invasive counterparts are known to be naturalised somewhere—the invasive ones had smaller genomes. We also found that species with more genes were more likely to be invasive. In plants, invasive species often possess expanded gene families that can provide them with a wider range of potential genes to adapt to various environments (Roddy et al., 2020). Expanded gene families can also improve the abilities of insects to resist pesticides, adapt to hosts and utilise nutrients (Huang et al., 2021). These characteristics are likely to promote invasiveness.

5 | CONCLUSIONS

We here identified the world's 100 worst invasive alien insect species. Moreover, we showed for the first time, using a multi-species comparative approach, that invasive insects differ in several species characteristics from related non-invasive insects. We found that invasive species typically are habitat generalists with high fecundity, short lifespans and fast development. For other variables such as female body size and number of enemies, the association with invasiveness was context dependent. While our study provides a first attempt to identify the characteristics of invasive insects, it also showed that for many species information on potentially relevant characteristics is not yet available. Therefore, more comparative studies are needed to identify characteristics of invasive insects. Ultimately, when more data have become available, the traits associated with invasiveness could be used to develop risk assessment for invasive alien insects.

AUTHOR CONTRIBUTIONS

The experimental design and idea were conceived by Zihua Zhao, Cang Hui and Mark van Kleunen. Data collection and arrangements was conducted by Zihua Zhao, Shuo Peng and Shanqing Yi. Statistical analyses were performed by Zihua Zhao. Zihua Zhao, Mark van Kleunen, Cang Hui, Zhihong Li and Gadi V. P. Reddy wrote the first draft of the manuscript. All authors contributed critically to revisions of the draft and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We declare no competing interests.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.xksn02vmv> (Zhao et al., 2023). Additional Supporting Information will also be found in the online version of the article at the publisher's website.

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REFERENCES

- Bakbergenuly, I., Hoaglin, D. C., & Kulinskaya, E. (2020). Estimation in meta-analyses of response ratios. *BMC Medical Research Methodology*, 20, 1–24. <https://doi.org/10.1186/s12874-020-01137-1>
- Banks, N. C., Paini, D. R., Bayliss, K. L., & Hodda, M. (2015). The role of global trade and transport network topology in the human-mediated dispersal of alien species. *Ecology Letters*, 18, 188–199. <https://doi.org/10.1111/ele.12397>
- Bates, O. K., Ollier, S., & Bertelsmeier, C. (2020). Smaller climatic niche shifts in invasive than non-invasive alien ant species. *Nature Communications*, 11, 5213. <https://doi.org/10.1038/s41467-020-19031-1>
- Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., Wilson, J. R. U., & Richardson, D. M. (2011). A proposed unified framework for biological invasions. *Trends in Ecology and Evolution*, 26, 333–339. <https://doi.org/10.1016/j.tree.2011.03.023>
- Bonnamour, A., Gippet, J. M., & Bertelsmeier, C. (2021). Insect and plant invasions follow two waves of globalization. *Ecology Letters*, 24, 2418–2426. <https://doi.org/10.1111/ele.13863>
- Brocknerhoff, E., & Liebhold, A. (2017). Ecology of forest insect invasions. *Biological Invasions*, 19, 3141–3159. <https://doi.org/10.1007/s10530-017-1514-1>
- Capellini, I., Baker, J., Allen, W. L., Street, S. E., & Venditti, C. (2015). The role of life history traits in mammalian invasion success. *Ecology Letters*, 18, 1099–1107. <https://doi.org/10.1111/ele.12493>
- Catford, J. A., Wilson, J. R., Pyšek, P., Hulme, P. E., & Duncan, R. P. (2022). Addressing context dependence in ecology. *Trends in Ecology and Evolution*, 37, 158–170. <https://doi.org/10.1016/j.tree.2021.09.007>
- CBD. (2000). *Decision V/8. Alien species that threaten ecosystems, habitats or species*. UNEP/CBD/COP/5/8. Secretariat of the Convention on Biological Diversity.
- Centre for Agriculture and Biosciences International Compendium Invasive Species (CABI). (2021). *Compendium invasive species database*. <http://www.cabi.org/isc/>
- Courchamp, F., Chapuis, J. L., & Pascal, M. (2003). Mammal invaders on islands: Impact, control and control impact. *Biological Reviews*, 78, 347–383. <https://doi.org/10.1017/S1464793102006061>
- Crawley, M. J. (1987). What makes a community invulnerable? In A. J. Gray, M. J. Crawley, & P. J. Edwards (Eds.), *Colonization, succession and stability* (pp. 429–453). Blackwell Science.
- Crowder, D. W., & Snyder, W. E. (2010). Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. *Biological Invasions*, 12, 2857–2876. <https://doi.org/10.1007/s10530-010-9733-8>
- Cunningham, S. A., Crane, M. J., Evans, M. J., Hingee, K. L., & Lindenmayer, D. B. (2022). Density of invasive western honey bee (*Apis mellifera*) colonies in fragmented woodlands indicates potential for large impacts on native species. *Scientific Reports*, 12, 3603. <https://doi.org/10.1038/s41598-022-07635-0>
- de Almeida-Rocha, J. M., Peres, C. A., & Oliveira, L. C. (2017). Primate responses to anthropogenic habitat disturbance: A pantropical meta-analysis. *Biological Conservation*, 215, 30–38. <https://doi.org/10.1016/j.biocon.2017.08.018>
- Dehnen-Schmutz, K., Touza, J., Perrings, C., & Williamson, M. (2007). A century of the ornamental plant trade and its impact on invasion success. *Diversity and Distributions*, 13, 527–534. <https://doi.org/10.1111/j.1472-4642.2007.00359.x>
- Fahrner, S., & Aukema, B. H. (2018). Correlates of spread rates for introduced insects. *Global Ecology and Biogeography*, 27, 734–743. <https://doi.org/10.1111/geb.12737>
- Fournier, A., Penone, C., Pennino, M. G., & Courchamp, F. (2019). Predicting future invaders and future invasions. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 7905–7910. <https://doi.org/10.1073/pnas.1803456116>
- Gippet, J. M., & Bertelsmeier, C. (2021). Invasiveness is linked to greater commercial success in the global pet trade. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2016337118. <https://doi.org/10.1073/pnas.2016337118>
- Gougherty, A. V., & Davies, T. J. (2021). Towards a phylogenetic ecology of plant pests and pathogens. *Philosophical Transactions of the Royal Society B*, 376, 20200359. <https://doi.org/10.1098/rstb.2020.0359>
- Gray, M. E., Sappington, T. W., Miller, N. J., Moeser, J., & Bohn, M. O. (2009). Adaptation and invasiveness of western corn rootworm: Intensifying research on a worsening pest. *Annual Review of Entomology*, 54, 303–321. <https://doi.org/10.1146/annurev.ento.54.110807.090434>
- Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, 555, 175–182. <https://doi.org/10.1038/nature25753>
- Hedges, L. V., Gurevich, J., & Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156. [https://doi.org/10.1890/0012-9658\(1999\)080\[1150:TMAOR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1150:TMAOR]2.0.CO;2)
- Huang, C., Kun, L., Qian, W., Wang, S., Cao, X., Rui, H., Zhan, A., Chen, M., Yang, N., & Fei, L. (2021). InvasionDB: A genome and gene database of invasive alien species. *Journal of Integrative Agriculture*, 20, 191–200. [https://doi.org/10.1016/S2095-3119\(20\)63231-2](https://doi.org/10.1016/S2095-3119(20)63231-2)
- Hulme, P. E., Bacher, S., Kenis, M., Klotz, S., Kühn, I., Minchin, D., Nentwig, W., Olenin, S., Panov, V., & Pergl, J. (2008). Grasping at the routes of biological invasions: A framework for integrating pathways into policy. *Journal of Applied Ecology*, 45, 403–414. <https://doi.org/10.1111/j.1365-2664.2007.01442.x>
- Invasive Species Specialist Group of the IUCN Species Survival Commission. (2021). Global invasive species database. <http://www.issg.org/>
- Jelbert, K., Buss, D., McDonald, J., Townley, S., Franco, M., Stott, I., Jones, O., Salguero-Gómez, R., Buckley, Y., & Knight, T. (2019). Demographic amplification is a predictor of invasiveness among plants. *Nature Communications*, 10, 5602. <https://doi.org/10.1038/s41467-019-13556-w>
- Knight, C. A., Molinari, N. A., & Petrov, D. A. (2005). The large genome constraint hypothesis: Evolution, ecology and phenotype. *Annals of Botany*, 95, 177–190. <https://doi.org/10.1093/aob/mci011>
- Kwon, O., & Choi, M. B. (2020). Interspecific hierarchies from aggressiveness and body size among the invasive alien hornet, *Vespa velutina nigrithorax*, and five native hornets in South Korea. *PLoS One*, 15, e0226934. <https://doi.org/10.1371/journal.pone.0226934>
- Labrie, G., Lucas, E., & Coderre, D. (2006). Can developmental and behavioural characteristics of the multicolored Asian lady beetle *Harmonia axyridis* explain its invasive success? *Biological Invasions*, 8, 743–754. <https://doi.org/10.1007/s10530-005-3428-6>
- Lajeunesse, M. J. (2015). Bias and correction for the log response ratio in ecological meta-analysis. *Ecology*, 96, 2056–2063. <https://doi.org/10.1890/14-2402.1>

- Leffler, A. J., James, J. J., Monaco, T. A., & Sheley, R. L. (2014). A new perspective on trait differences between native and invasive exotic plants. *Ecology*, 95, 298–305. <https://doi.org/10.1890/13-0102.1>
- Levin, S. C., Crandall, R. M., Pokoski, T., Stein, C., & Knight, T. M. (2020). Phylogenetic and functional distinctiveness explain alien plant population responses to competition. *Proceedings of the Royal Society B*, 287, 20201070. <https://doi.org/10.1098/rspb.2020.1070>
- Liebholt, A. M., Turner, R. M., Blake, R. E., Bertelsmeier, C., Brockerhoff, E. G., Nahrung, H. F., Pureswaran, D. S., Roques, A., Seebens, H., & Yamanaka, T. (2021). Invasion disharmony in the global biogeography of native and non-native beetle species. *Diversity and Distributions*, 27, 2050–2062. <https://doi.org/10.1111/ddi.13381>
- Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, 20, 223–228. <https://doi.org/10.1016/j.tree.2005.02.004>
- Lounibos, L. P. (2002). Invasions by insect vectors of human disease. *Annual Review of Entomology*, 47, 233–266. <https://doi.org/10.1146/annurev.ento.47.091201.145206>
- Moritz, R. F., Härtel, S., & Neumann, P. (2005). Global invasions of the western honeybee (*Apis mellifera*) and the consequences for biodiversity. *Ecoscience*, 12, 289–301. <https://doi.org/10.2980/i1195-6860-12-3-289.1>
- Nakagawa, S., Lagisz, M., Jennions, M. D., Koricheva, J., Noble, D. W., Parker, T. H., Sánchez-Tójar, A., Yang, Y., & O'Dea, R. E. (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13, 4–21. <https://doi.org/10.1111/2041-210X.13724>
- National Center for Biotechnology Information. (2021). <https://www.ncbi.nlm.nih.gov/>
- Novoa, A., Richardson, D. M., Pyšek, P., Meyerson, L. A., Bacher, S., Canavan, S., Catford, J. A., Čuda, J., Essl, F., & Foxcroft, L. C. (2020). Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. *Biological Invasions*, 22, 1801–1820. <https://doi.org/10.1007/s10530-020-02220-w>
- Nunez-Mir, G. C., Guo, Q., Rejmánek, M., Iannone, B. V., III, & Fei, S. (2019). Predicting invasiveness of exotic woody species using a traits-based framework. *Ecology*, 100, e02797. <https://doi.org/10.1002/ecy.2797>
- Origin Lab. (2021). *Origin (Pro)*, Version 2021b. OriginLab Corporation.
- Pagad, S., Genovesi, P., Carnevali, L., Schigel, D., & McGeoch, M. A. (2018). Introducing the global register of introduced and invasive species. *Scientific Data*, 5, 1–12. <https://doi.org/10.1038/sdata.2017.202>
- Palma, E., Vesik, P. A., White, M., Baumgartner, J. B., & Catford, J. A. (2021). Plant functional traits reflect different dimensions of species invasiveness. *Ecology*, 102, e03317. <https://doi.org/10.1002/ecy.3317>
- Pandit, M. K., White, S. M., & Pockock, M. J. (2014). The contrasting effects of genome size, chromosome number and ploidy level on plant invasiveness: A global analysis. *New Phytologist*, 203, 697–703. <https://doi.org/10.1111/nph.12799>
- Preziosi, R. F., Fairbairn, D. J., Roff, D. A., & Brennan, J. M. (1996). Body size and fecundity in the waterstrider *Aquarius remigis*: A test of Darwin's fecundity advantage hypothesis. *Oecologia*, 108, 424–431. <https://doi.org/10.1007/BF00333717>
- Pyšek, P., Manceur, A. M., Alba, C., McGregor, K. F., Pergl, J., Štajerová, K., Chytrý, M., Danihelka, J., Kartesz, J., & Klimešová, J. (2015). Naturalization of central European plants in North America: Species traits, habitats, propagule pressure, residence time. *Ecology*, 96, 762–774. <https://doi.org/10.1890/14-1005.1>
- R Core Team. (2020). *RStudio: Integrated development for R*. RStudio, PBC. <http://www.rstudio.com/>
- Renault, D., Laparie, M., McCauley, S. J., & Bonte, D. (2018). Environmental adaptations, ecological filtering, and dispersal central to insect invasions. *Annual Review of Entomology*, 63, 345–368. <https://doi.org/10.1146/annurev-ento-020117-043315>
- Ricciardi, A. (2007). Are modern biological invasions an unprecedented form of global change? *Conservation Biology*, 21, 329–336. <https://doi.org/10.1111/j.1523-1739.2006.00615.x>
- Riera, M., Pino, J., & Melero, Y. (2021). Impact of introduction pathways on the spread and geographical distribution of alien species: Implications for preventive management in Mediterranean ecosystems. *Diversity and Distributions*, 27, 1019–1034. <https://doi.org/10.1111/ddi.13251>
- Roddy, A. B., Théroux-Rancourt, G., Abbo, T., Benedetti, J. W., Brodersen, C. R., Castro, M., Castro, S., Gilbride, A. B., Jensen, B., & Jiang, G. F. (2020). The scaling of genome size and cell size limits maximum rates of photosynthesis with implications for ecological strategies. *International Journal of Plant Sciences*, 181, 75–87. <https://doi.org/10.1086/706186>
- Schwarzer, G., Carpenter, J. R., & Rücker, G. (2015). *Meta-analysis with R (Use-R!)*. Springer International Publishing.
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., van Kleunen, M., & Winter, M. (2018). Global rise in emerging alien species results from increased accessibility of new source pools. *Proceedings of the National Academy of Sciences of the United States of America*, 115, E2264–E2273. <https://doi.org/10.1073/pnas.1719429115>
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.
- Tayeh, A., Hufbauer, R., Estoup, A., Ravigné, V., Frachon, L., & Faconet, B. (2015). Biological invasion and biological control select for different life histories. *Nature Communications*, 6, 7268. <https://doi.org/10.1038/ncomms8268>
- Thomas, S. M., Simmons, G. S., & Daugherty, M. P. (2017). Spatiotemporal distribution of an invasive insect in an urban landscape: Introduction, establishment and impact. *Landscape Ecology*, 32, 2041–2057. <https://doi.org/10.1007/s10980-017-0565-0>
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525, 100–103. <https://doi.org/10.1038/nature14910>
- van Kleunen, M., Weber, E., & Fischer, M. (2010). A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, 13, 235–245. <https://doi.org/10.1111/j.1461-0248.2009.01418.x>
- Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48. <https://doi.org/10.18637/jss.v036.i03>
- Zhao, Z., Hui, C., Peng, S., Yi, S., Li, Z., Reddy, G. V. P., & van Kleunen, M. (2023). The world's 100 worst invasive alien insect species. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.xksn02vmv>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. The differences of pathways between invasive and non-invasive species.

Figure S2. The differences of habitats between invasive and non-invasive species.

Figure S3. The differences of female body size between invasive and non-invasive species.

Figure S4. The differences of adult lifespan between invasive and non-invasive species.

Figure S5. The differences of growth degree-days (i.e. effective accumulated temperature) from egg to adult between invasive and non-invasive species.

Figure S6. The differences of fecundity capacity (average number of eggs laid per female during the whole life time) between invasive and non-invasive species.

Figure S7. The differences of voltinism (number of generations per year) between invasive and non-invasive species.

Figure S8. The differences of enemies between invasive and non-invasive species.

Figure S9. The differences of genome size between invasive and non-invasive species.

Figure S10. The differences of genes between invasive and non-invasive species.

Table S1. The questionnaire survey of invasive alien insects.

Appendix S1. The complete species list of naturalised alien insects globally.

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