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Fewer non-native insects in freshwater than in terrestrial habitats across continents

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Abstract

Aim: Biological invasions are a major threat to biodiversity in aquatic and terrestrial habitats. Insects represent an important group of species in freshwater and terrestrial habitats, and they constitute a large proportion of non-native species. However, while many non-native insects are known from terrestrial ecosystems, they appear to be less represented in freshwater habitats. Comparisons between freshwater and terrestrial habitats of invader richness relative to native species richness are scarce, which hinders syntheses of invasion processes. Here, we used data from three regions on different continents to determine whether non-native insects are indeed under-represented in freshwater compared with terrestrial assemblages.

Location: Europe, North America, New Zealand.

Methods: We compiled a comprehensive inventory of native and non-native insect species established in freshwater and terrestrial habitats of the three study regions. We then contrasted the richness of non-native and native species among freshwater and terrestrial insects for all insect orders in each region. Using binomial regression, we analysed the proportions of non-native species in freshwater and terrestrial

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habitats. Marine insect species were excluded from our analysis, and insects in low-salinity brackish water were considered as freshwater insects.

Results: In most insect orders living in freshwater, non-native species were under-represented, while they were over-represented in a number of terrestrial orders. This pattern occurred in purely aquatic orders and in orders with both freshwater and terrestrial species. Overall, the proportion of non-native species was significantly lower in freshwater than in terrestrial species.

Main conclusions: Despite the numerical and ecological importance of insects among all non-native species, non-native insect species are surprisingly rare in freshwater habitats. This is consistent across the three investigated regions. We review hypotheses concerning species traits and invasion pathways that are most likely to explain these patterns. Our findings contribute to a growing appreciation of drivers and impacts of biological invasions.

KEYWORDS
aquatic insects, biological invasions, established species, freshwater, insect invasions, life history traits, pathways, species richness, terrestrial insects

1 | INTRODUCTION

Biological invasions are an important component of global change (IPBES, 2019; Pyšek et al., 2020) and a well-recognized threat to biodiversity in both terrestrial (D'Antonio & Kark, 2002) and aquatic habitats (Francis & Chadwick, 2021; Jackson et al., 2017). Freshwater ecosystems are not only highly invaded (Bolpagni, 2021; Pyšek et al., 2010) but also very susceptible to severe impacts of invasive species (Moorhouse & Macdonald, 2015; Sala et al., 2000). Macroinvertebrates are common and often damaging invaders of freshwater ecosystems worldwide (Baur & Schmidlin, 2007; Cuthbert et al., 2021; Emery-Butcher et al., 2020; Ricciardi, 2015). However, the representation of different higher-level taxa among non-native aquatic invertebrates is unbalanced (Ricciardi, 2015), and Fenoglio et al. (2016) proposed that invasions by insects are less successful in freshwater, when compared with terrestrial habitats. Similarly, insects have fewer non-native representatives than other groups of freshwater invertebrates such as crustaceans and molluscs (Fenoglio et al., 2016; Karatayev et al., 2009; Ricciardi, 2015; Strayer, 2010).

This imbalance is surprising as insects are a highly species rich, diverse and ubiquitous taxon (Chapman, 2009; Stork, 2018) occurring in nearly all terrestrial and freshwater habitats. Furthermore, non-native insects vastly outnumber other invertebrates and vertebrates in species richness (Roques et al., 2010; Seebens et al., 2017, 2018). However, Liebhold et al. (2016) suggested that insect orders that are dominated by aquatic species (i.e. Ephemeroptera, Odonata, Plecoptera or Trichoptera) have relatively few non-native representatives. Yet, it is unclear whether this pattern also occurs among insect orders comprising both terrestrial and aquatic species. Moreover, to our knowledge, the question whether aquatic insects are indeed less common as invaders than terrestrial insects has not been explicitly investigated on a large taxonomic and geographic scale.

The number of established non-native species is increasing worldwide (Seebens et al., 2017), and so is the colonization by aquatic and terrestrial invertebrates (Baur & Schmidlin, 2007; Brockerhoff & Liebhold, 2017; Ricciardi, 2006). Exploring patterns of invasions across habitats can advance our understanding of invasion processes and drivers and provide crucial information informing efforts to mitigate future invasions.

Here, we provide the first comprehensive quantitative assessment of the relative success of freshwater and terrestrial insect invaders at a large geographical scale. We examined the proportions of established non-native freshwater and terrestrial insects relative to the number of corresponding native species across three major geographic regions. In particular, we analysed whether freshwater non-native insects are indeed less likely to invade than terrestrial insects and whether this is a universal phenomenon across all insect orders and across continental regions (Europe, North America and Australasia i.e. New Zealand). We elaborated on these results with regard to hypotheses related to life history traits, habitat specifics and invasion pathways which may explain such differences between freshwater and terrestrial insects. Finally, although there are very few truly marine insects (Cheng, 2009), for completeness, we also discuss invasions of marine insect species.

2 | METHODS

2.1 | Data compilation

We collected data on the numbers of native and non-native insect species. In compiling lists of non-native species, we only considered established non-native species with self-sustaining populations outdoors (Colautti & MacIsaac, 2004; Pyšek et al., 2004). Our datasets did not include non-native species which, to our knowledge, occur only in indoor conditions including aquaria and greenhouses. Species lists were collected for freshwater and terrestrial habitats in Europe, North America and New Zealand, respectively, for which comprehensive lists of native and non-native insect species are available. We also compiled information on insect species in marine habitats and on the presence of non-native marine insect species to ensure that we did not include marine species in our freshwater or terrestrial lists. However, because the number of strictly marine insect species is very small (Table S1) and because our focus here is on the comparison of invasions of freshwater and terrestrial insects, we do not elaborate on marine species in great detail, and we did not include them as a separate category in the analysis.

The information we gathered was assembled from multiple published species inventories (including de Jong et al., 2014; Foottit & Adler, 2017; Liebhold et al., 2016; Simpson & Eyler, 2018; Turner, Brockerhoff, et al., 2021; Yamanaka et al., 2015; all of which have been compiled recently in an online database, Turner, Blake, & Liebhold, 2021), books (Macfarlane et al., 2010; Merritt et al., 2008; Merritt & Cummins, 1996) and online databases (DAISIE and EASIN databases; Roques et al., 2010, 2016) and freshwaterecology.info (Schmidt-Kloiber & Hering, 2015) (for details see Text S1). For marine insect species, we searched Macfarlane et al. (2010), Merritt and Cummins (1996), Merritt et al. (2008) and the DAISIE and EASIN databases (Roques et al., 2010, 2016) as well as the AquaNIS marine invasions database (AquaNIS, 2015) and the Alien Species First Records Database (Seebens, 2020; Seebens et al., 2018). We standardized taxonomic information according to the GBIF Backbone Taxonomy (GBIF Secretariat, 2021), with the exception of the order Psocodea which we kept as two separate orders, Phthiraptera and Psocoptera, as they have been treated traditionally. In this way, we obtained 29 orders with at least one species, either native or non-native (Tables S2 and S3).

There is no single rigorous definition of what constitutes an aquatic vs. a terrestrial insect species. In fact, definitions of aquatic and terrestrial insects differ greatly between studies (compare Merritt et al., 2008; Merritt & Cummins, 1996). Here, we applied a strict and a broad definition of freshwater aquatic species (while treating all others as “terrestrial”). In the “strict” definition, we consider as freshwater insects those species which spend at least one stage of their life cycle obligatorily in freshwater environments. This definition encompasses insects living on the surface of lotic and lentic water bodies, including temporal habitats such as puddles or water-filled tree holes. In the “broad” definition, we also included insects occupying semi-aquatic habitats such as the edges of water bodies, or algal mats, species specialized on feeding on hydrophytes (including burrowers and miners) in submergent, emergent and floating zones, or living in water-saturated substrates such as wet soil or wood, or sap flows. For the broad dataset, we also included parasitoids known or suspected to attack hosts under the water surface (Burghele, 1959; Merritt & Cummins, 1996). In both of these classification systems, insects feeding on terrestrial vegetation growing in proximity to water bodies and parasitoids of terrestrial stages of aquatic insects were not considered aquatic (Merritt & Cummins, 1996; Merritt et al., 2008).

2.2 | Data analysis and presentation

To compare numbers of non-native and native insect species in freshwater and terrestrial habitats, we computed the total number of native and non-native species, in both kinds of habitat, for each of the three regions and insect orders. The overall ratio of non-native to native freshwater and terrestrial species was compared using Chi-square tests. For each of the three regions, we created a contingency table with two groups representing habitat (freshwater vs. terrestrial) and two categories representing status (native vs. established non-native). Then, we compiled these values by insect order. For this, we overlaid a plot showing the number of freshwater and terrestrial species in each order with a line representing the number of non-native species per order that would be expected if they were in the same proportions as all the non-native species to all the native species in the region. We calculated a 95% prediction interval based on a binomial distribution under the assumption that the proportions of non-native and native species in a given order are identical to the overall proportions in each of the regional datasets. Insect orders that were located above or below the line and outside of the confidence intervals were considered over- or under-represented, respectively, in terms of the number of non-native species.

We compared non-native to native species ratios in freshwater and terrestrial habitats using a generalized mixed effect regression model with binomial error distribution and a probit link function. Insect order was accounted for by including it as a random term. As fixed effects, we used regions (Europe, North America and New Zealand), habitat (freshwater and terrestrial) and their interaction. We ensured that the applied models have substantial support by applying a single-term backward selection process based on likelihood ratio testing and by comparing values of the Akaike information criterion (AIC; Burnham & Anderson, 2004) and model residuals (Table S4, Figures S1 and S2). No terms were nonsignificant, and therefore, none were removed. To conduct pairwise comparisons of habitats across the regions, we estimated and contrasted marginal means (Kaltenbach, 2021) with a Benjamini & Hochberg correction for multiplicity adjustment (Benjamini & Hochberg, 1995). All analyses were made in R version 4.0.5 (R Core Team, 2021). We computed regression models using the “glmmTMB” package (Magnusson et al., 2017) and used the “DHARMa” package (Hartig, 2021) to examine the residuals. Pairwise comparisons of marginal means were performed using the “emmeans” package (Lenth, 2021).

3 | RESULTS

3.1 | All freshwater versus terrestrial insects

Overall, freshwater insects are much less species rich than terrestrial insects, in both native and non-native species (Figures 1–3; Figure S3; Table S5). Moreover, the numbers of non-native species were considerably lower relative to the numbers of native species across all regions, which was reflected in the small ratios of non-native to native species numbers (almost 10-fold in Europe and North America and almost fourfold in New Zealand; Table 1; Figure 2). The results were similar using the broad dataset (Table 1; Figures 2 and 3). Our search for marine insects revealed a total of only 20 insect species in North America, six insect species in New Zealand and at least six insect species in Europe that are strictly marine (i.e. living *in* the water in marine ecosystems and not just in terrestrial habitats on the sea shore) (Table S1). Because of their scarcity, and because our focus here is on the comparison of terrestrial and freshwater insects, strictly marine species were excluded from our analysis.

3.2 | Comparison at the level of insect orders

At the order level, we found that many of the freshwater insects were significantly under-represented in terms of their proportions of non-native species (i.e. they fell below the expectation line and outside the 95% prediction interval, Figure 1). Among them were orders that are purely or almost purely aquatic (e.g. Ephemeroptera, Plecoptera and Trichoptera) as well as aquatic subsets of the larger orders that contain both freshwater and terrestrial species (e.g. Coleoptera and Diptera). By contrast, non-native species were over-represented in numerous purely terrestrial insect orders (e.g. Blattodea, Hemiptera, Phthiraptera, Psocoptera, and Thysanoptera) (i.e. they fell above the expectation line and outside the 95% prediction interval, Figure 1). These patterns were broadly similar across the three regions. Likewise, the results were comparable for the strict and broad datasets, although some groups (e.g. aquatic Coleoptera) shifted slightly (Figure 1).

The mean proportions across insect orders of non-native species (out of all species) were significantly lower for freshwater insects than for terrestrial insects, and this was consistent across the three regions (Table 2; Figures 2 and 3; Table S4). The difference between non-native freshwater and terrestrial species was only marginally nonsignificant for the strict dataset from New Zealand, while there was a significant difference for the broad dataset (Table S5; Figure 3).

3.3 | Taxa most represented among invaders

Diptera stand out as the most species-rich group of non-native freshwater insects in all three regions, whereas Coleoptera, Hemiptera and Hymenoptera dominate in terrestrial habitats (Figure 1; Figure S2, Table S2). Prominent dipteran families among non-native freshwater insects are the Culicidae (mosquitoes), Chironomidae (nonbiting midges) and Syrphidae (hover flies). There is surprisingly little overlap among the invasive freshwater species across the regions (Table S3). Only five of 81 strictly aquatic invasive freshwater species (the Asian tiger mosquito, *Aedes albopictus*, the Asian bush mosquito, *Aedes japonicus*, the southern house mosquito, *Culex quinquefasciatus*, the common drone fly, *Eristalis tenax*, and the Hydrilla leafcutter moth, *Parapoynx diminutalis*) occur in more than one of the three investigated regions. Despite the prominence of non-native freshwater Diptera, they are consistently under-represented relative to the number of native species (Figure 1). Even though Odonata are a comparatively small order, they are the second-most common order of freshwater invaders in New Zealand and North America (although they are absent in Europe) (Figure 1, Table S3). Of the other typical freshwater insect orders, only two species of mayflies (Ephemeroptera) are among the non-native species, both in North America.

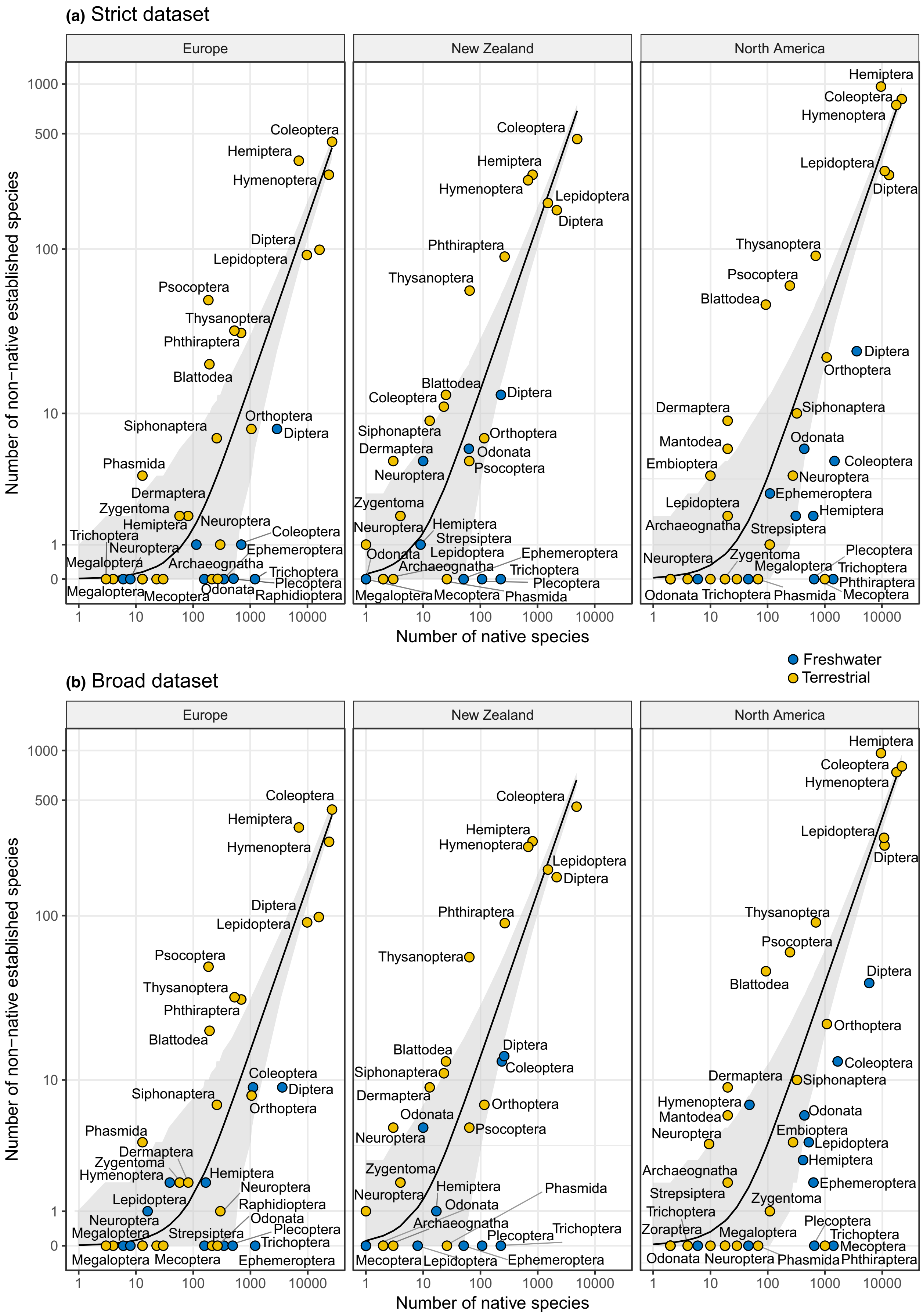
4 | DISCUSSION

4.1 | Main findings

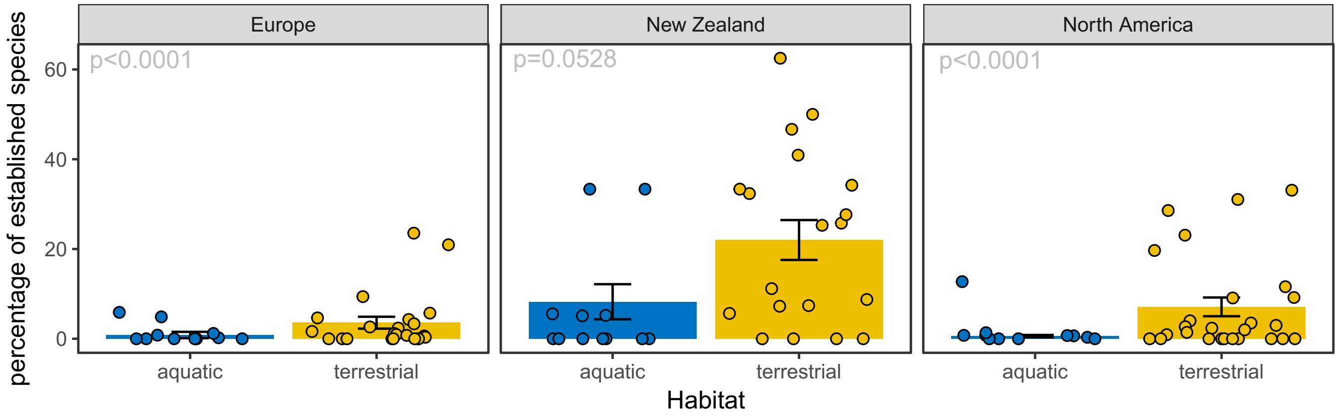
Our analyses show that freshwater insects are consistently under-represented compared with terrestrial species in terms of their numbers of non-native species relative to native species. This was evident in the non-native to native species ratios which were considerably lower in freshwater than in terrestrial insects. This pattern occurred in purely aquatic orders as well as orders which contain both freshwater and terrestrial representatives. And it was consistent across the three study regions (Europe, North America and New Zealand), which indicates that this under-representation of non-native freshwater insects is occurring at a large geographical scale and may be inherent and generalizable across insects overall. Our findings are remarkable because insects (in general) are the most species-rich class (Chapman, 2009; Stork, 2018), and they are more numerous as established non-native species than any other animal group (Seebens et al., 2017, 2018). However, despite the high richness of freshwater insects (Balian et al., 2008; Dijkstra et al., 2014) and their high abundance in all kinds of freshwater habitats (Hershey et al., 2001), there are surprisingly few freshwater insect species that have invaded non-native regions. Moreover, hardly any invasive freshwater insect species have invaded more than one of the regions we studied.

An apparent paucity of non-native freshwater insects has been noted previously, mainly in comparison with other groups of macroinvertebrates, such as Crustacea or Mollusca (Fenoglio et al., 2016; Ricciardi, 2015; Strayer, 2010), rather than in comparison with

FIGURE 1 Numbers of native versus non-native species per insect order in freshwater (blue) and terrestrial (yellow) habitats across the three investigated regions (Europe, New Zealand and North America). Solid lines represent the expected number of non-native species assuming that the proportions of non-native and native species in a given order are identical to the overall proportions in each of the regional datasets. The shading represents the 95% confidence interval, based on the binomial distribution. Orders located outside of the shaded range are considered under- or over-represented. Panels (a) and (b) represent analyses based on datasets with strict and broad definitions of aquatic insects, respectively


(a) Strict dataset
Europe
New Zealand
North America
Number of non−native established species
Number of native species
1000
500
100
10
1
0
1
10
100
1000
10000
Coleoptera
Hemiptera
Hymenoptera
Diptera
Lepidoptera
Psocoptera
Thysanoptera
Phthiraptera
Blattodea
Orthoptera
Siphonaptera
Phasmida
Dermaptera
Zygentoma
Neuroptera
Trichoptera
Megaloptera
Archaeognatha
Ephemeroptera
Plecoptera
Odonata
Mecoptera
Raphidioptera
Strepsiptera
Mantodea
Embioptera
Freshwater
Terrestrial
(b) Broad dataset
Europe
New Zealand
North America
Number of non−native established species
Number of native species
Coleoptera
Hemiptera
Hymenoptera
Diptera
Lepidoptera
Psocoptera
Thysanoptera
Phthiraptera
Blattodea
Orthoptera
Siphonaptera
Phasmida
Dermaptera
Zygentoma
Neuroptera
Raphidioptera
Odonata
Strepsiptera
Plecoptera
Trichoptera
Megaloptera
Mecoptera
Ephemeroptera
Archaeognatha
Mantodea
Embioptera
Zoraptera

(a) Strict dataset



(b) Broad dataset

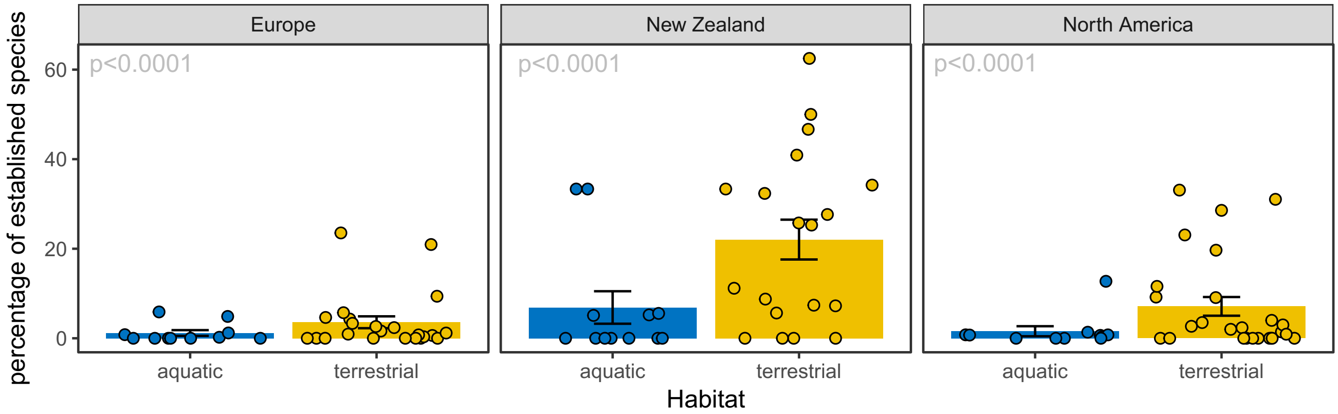


FIGURE 2 Percentages (calculated from proportions) of non-native, established species (out of all species) in freshwater and terrestrial habitats across the three investigated regions (Europe, New Zealand and North America). The error bars represent the standard error around the mean across the insect orders. Datapoints represent percentages of given orders. *p*-Values indicating differences between the proportions of freshwater and terrestrial species within regions are obtained from marginal means contrasts. Panels (a) and (b) represent analyses based on datasets with strict and broad definitions of aquatic insects, respectively

terrestrial insects. Other studies have concluded that there are very few invaders among freshwater insects despite their high species richness in the native freshwater fauna (Karatayev et al., 2009; Ricciardi, 2015). However, our study is the first to quantitatively demonstrate that the hypothesis that freshwater insects are less successful as invaders (Fenoglio et al., 2016) is actually true, and it is the first to compare data across several biogeographically distinct regions. This is relevant because there are very few comparisons between freshwater and terrestrial habitats in terms of the richness of invaders relative to the richness of native species (e.g. Liebhold et al., 2016).

4.2 | Potential confounding factors

4.2.1 | Marine insects

Although not within the main scope of our study, we also reviewed marine non-native and native insects. Definitions of marine insects vary widely and may include species that live on the mainly terrestrial part of the sea shore (e.g. on washed-up marine debris) while others define marine insects as only those which spend at least part their life cycle between the upper intertidal and the open ocean (e.g. Cheng, 2009). By our definitions of aquatic and terrestrial insects, we consider insects occurring on marine debris on the sea shore as terrestrial as they do not have proper aquatic life stages. We considered only purely marine species, such as marine water striders in the genus *Halobates* (Cheng, 2009) and certain strictly marine chironomids (Brodin & Andersson, 2009; Paasivirta, 2014), as marine and excluded them from our analyses of freshwater and terrestrial insects. However, as the number of truly marine species is very small in the three regions we investigated (especially relative to the number of terrestrial and freshwater insects) (Brodin & Andersson, 2009; Cheng, 2009; Paasivirta, 2014), their exclusion from our analyses does not affect our findings and conclusions. Species occurring in brackish water are somewhat ambiguous to categorize as they could be defined as occurring in both freshwater and marine habitats or only in one of these. This distinction is not easily made as taxa in brackish habitats may occur in only mildly saline water or in highly saline

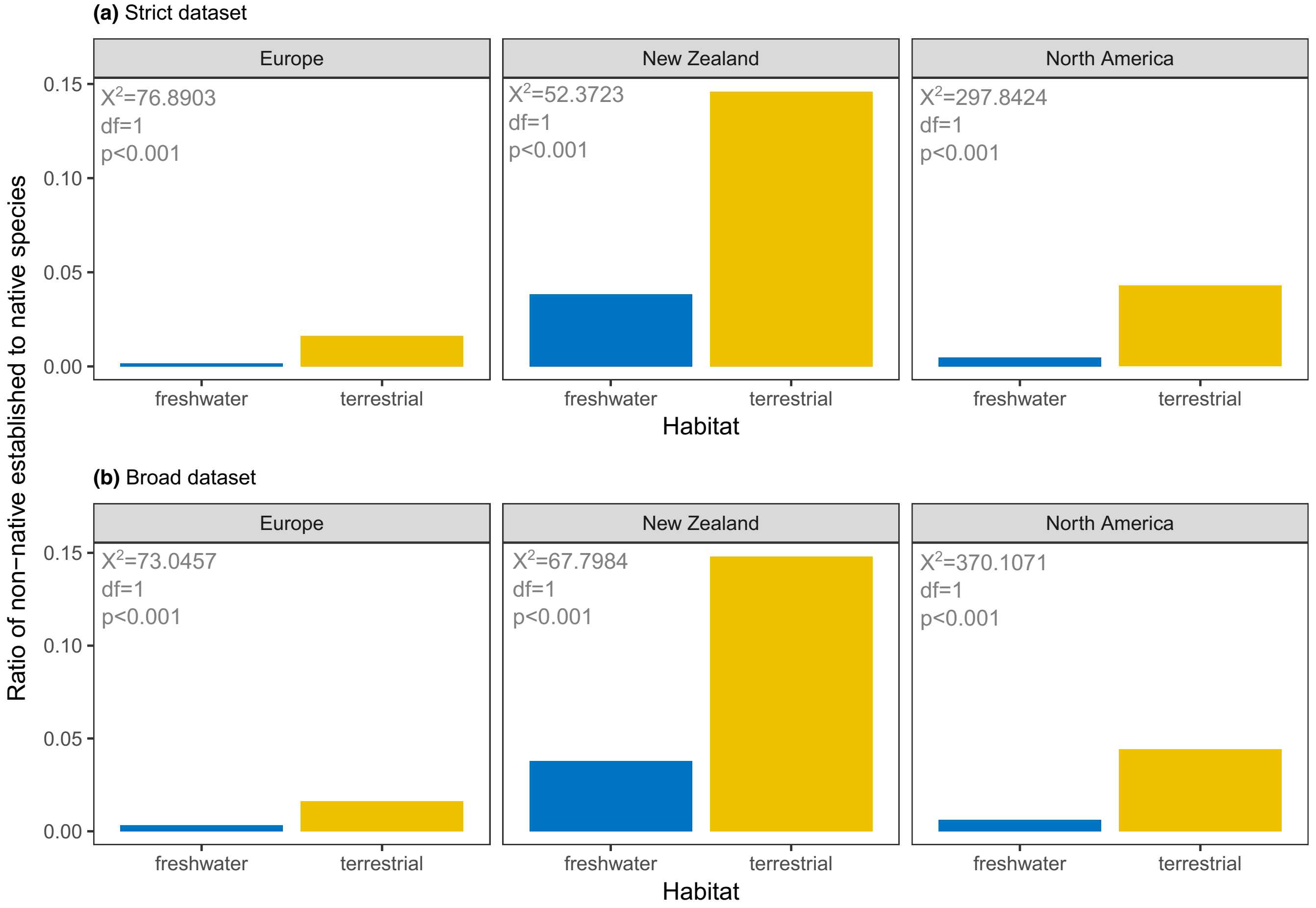


FIGURE 3 Ratio of non-native to native species in freshwater and terrestrial habitats. The ratios presented were calculated from the total numbers of freshwater and terrestrial species, for each of the regions, with statistics based on X^2 tests of independence. Panels (a) and (b) represent analyses based on datasets with strict and broad definitions of aquatic insects, respectively

TABLE 1 Overall numbers of freshwater and terrestrial native and non-native insects in Europe, New Zealand and North America and ratios of non-native to native species

Region	Habitat	Number of native species	Number of non-native species	Ratio non-native to native species
Strict dataset				
Europe	Freshwater	5971	10	0.0017
Europe	Terrestrial	87,645	1418	0.0162
New Zealand	Freshwater	703	28	0.0384
New Zealand	Terrestrial	10,751	1568	0.1458
North America	Freshwater	8696	37	0.0043
North America	Terrestrial	78,128	3359	0.0430
Broad dataset				
Europe	Freshwater	7135	23	0.0031
Europe	Terrestrial	86,481	1406	0.0163
New Zealand	Freshwater	923	35	0.0380
New Zealand	Terrestrial	10,531	1560	0.1481
North America	Freshwater	11,753	74	0.0063
North America	Terrestrial	75,071	3322	0.0442

TABLE 2 Summary of effects of habitat (freshwater versus terrestrial) and region (Europe, New Zealand and North America) on the ratio of non-native to native species in the insect orders

Predictors	Estimates	SE	*Z*-test	*p* Value
Strict dataset				
Intercept	−2.73	0.18	−15.51	**<.001**
Habitat (terrestrial)	0.49	0.10	4.70	**<.001**
Region (New Zealand)	1.33	0.14	9.378	**<.001**
Region (North America)	0.24	0.12	2.04	**.041**
Habitat (terrestrial) × Region (New Zealand)	−0.29	0.14	−2.03	**.042**
Habitat (terrestrial) × Region (North America)	0.14	0.12	1.26	.207
N/*G*	101/28 (Orders)			
Marginal R^2/Conditional R^2	0.353/0.996			
AIC	1014.907			
Broad dataset				
Intercept	−2.58	0.16	−16.05	**<.001**
Habitat (terrestrial)	0.33	0.07	4.40	**<.001**
Region (New Zealand)	1.04	0.11	9.42	**<.001**
Region (North America)	0.21	0.08	2.53	**.011**
Habitat (terrestrial) × Region (New Zealand)	0.01	0.11	0.09	.931
Habitat (terrestrial) × Region (North America)	0.18	0.09	2.11	**.035**
N/*G*	101/28 (Orders)			
Marginal R^2/Conditional R^2	0.310/0.995			
AIC	1051.500			

Note: The table represents the outcome of the binomial regression analysis of the strict and broad datasets. In this analysis, the data from Europe were used as the reference point, so that the estimates shown are relative to the results for Europe.

Abbreviations: AIC, Akaike criterion; Conditional R^2, the proportion of variance explained by both fixed and random effects; *G*, number of groups; Marginal R^2, the proportion of variance explained by the fixed effect; *N*, number of observations; SE, standard error of the coefficient estimate.

water and can include species that are euryhaline which tolerate a wide range of salinity values. However, as many of the species occurring in brackish water with lower salinity, such as eastern and north-eastern parts of the Baltic Sea, are present also in freshwater habitats, we considered them as freshwater insects.

4.2.2 | Potential sampling biases

As freshwater habitats may be more difficult to study than terrestrial habitats (for reasons such as greater difficulty of access by researchers) and because there are probably more researchers studying terrestrial than freshwater habitats, there could be sampling bias in favour of terrestrial invasive species (i.e. invaders in freshwater habitats may have been overlooked more than those in terrestrial habitats). However, as non-native species other than insects (such as molluscs, crustaceans and fish) occurring in freshwater habitats are well known and numerous (Karatayev et al., 2009; Ricciardi, 2015), this bias is unlikely to affect our findings to more than a minor extent. Furthermore, a study of fish invasions in North America found that the observed invasion pattern is not a result of bias associated with human population density (which can be considered a proxy for sampling effort) (Davis & Darling, 2017).

4.2.3 | Geographic limitations

We acknowledge there are certain geographical limitations to our study, especially as we were unable to source comprehensive information on other world regions such as parts of Africa, Asia and South America, a common problem of global biodiversity and invasion studies (Hughes et al., 2021; Pyšek et al., 2008). However, our study is based on comprehensive inventories spanning across three distant world regions (Europe, North America and New Zealand) whose insect biodiversity and invasions are well-studied. Given the consistent patterns we detected, this suggests that our findings are applicable at least for temperate and boreal regions and that this under-representation of non-native freshwater insects is likely to be a universal pattern. Nevertheless, to improve and broaden future approaches, it is crucial for future studies to bridge information availability across all world regions and to intensify research in regions and habitats where detailed species inventories are less comprehensive.

4.3 | Drivers and mechanisms

The mechanisms responsible for the limited success of freshwater insects as invaders are not fully understood. However, based on theoretical considerations and the characteristics of the few freshwater insect species that succeeded to invade, a number of hypotheses can be discussed.

4.3.1 | Transport pathways and interactions

Transport pathways typically involved in invasions of aquatic species and the relative unsuitability of these pathways for freshwater insects (compared with other freshwater species) are likely to play a key role. Several recent studies highlighted the importance of pathways in insect invasions (Liebhold et al., 2012, 2016; Ricciardi, 2006; Turner, Brockerhoff, et al., 2021). While numerous terrestrial non-native insects are being transported with their host plants via trade in plant products and live plants (Brockerhoff & Liebhold, 2017; Liebhold et al., 2012), this is thought to be a less likely pathway for aquatic insects (Fenoglio et al., 2016), the latter being generally much less associated with specific host plants. For example, numerous species of terrestrial Thysanoptera, an over-represented terrestrial order (see Figure 1; Figure S1), are transported with their crop or ornamental host-plants (Liebhold et al., 2016, 2018). By contrast, we observed only a single representative of a semi-aquatic Thysanoptera (*Organothrips indicus*) (in Europe). However, this species, along with nine herbivorous Crambidae (Lepidoptera) in the genera *Agassiziella*, *Elophila* and *Parapoynx*, were not included in the analysis because these were reported only in indoor habitats (Roques et al., 2016), and consequently, we did not consider them as established in the wild. Another aspect of the life cycle of freshwater insects that may impede invasions is their lack of adaptations amenable to long distance transport via shipping (e.g. with ballast water; Duggan et al., 2006; Karatayev et al., 2009; Liebhold et al., 2016). Aquatic invertebrates with numerous non-native species, such as crustaceans and molluscs, often have life stages that are adapted to transport with ballast water (e.g. durable eggs or planktonic larval stages or drought-resistance in adult stages), a trait known to facilitate invasions (Panov et al., 2004; Ricciardi, 2015). Most freshwater insects lack adaptations that would enable them to tolerate conditions that prevail in ballast water, such as low oxygen levels (Fenoglio et al., 2016). However, some representatives of the Diptera, such as mosquitoes (Culicidae), are well adapted to low oxygen conditions and consequently are easily transported and can survive even in small amounts of water (Benedict et al., 2007; Ibañez-Justicia, 2020; Medlock et al., 2012). Hitchhiking at the egg stage in substrates without biological significance such as used tyres and ornamental plants (e.g. "lucky bamboo" *Dracaena* spp.) is a common pattern favouring invasion in dipteran species such as the tiger mosquito, *Aedes albopictus* (Linthicum et al., 2003; Rabitsch, 2010).

4.3.2 | Life cycle adaptations and habitat requirements

Differences in life cycle adaptations and habitat requirements facilitating invasions are also likely to be involved in the lower invasion success of freshwater insects. Asexual reproduction such as parthenogenesis is very common among terrestrial non-native insects (and freshwater invaders such as molluscs) (Brockerhoff & Liebhold, 2017; Karatayev et al., 2009; Lee et al., 2005; Peacock & Worner, 2008), but it appears to be generally rare in freshwater insects (de Moor, 1992; Fenoglio et al., 2016). However, asexual reproduction occurs in some freshwater insects such as certain Odonata (e.g. de Moor, 1992; Lorenzo-Carballa et al., 2011, 2012), one of few freshwater orders that includes successful invaders (Tables S2 and S3), as well as in some mayflies (Liegeois et al., 2021).

Because most freshwater insects have an aquatic and a terrestrial stage, they require suitable freshwater and terrestrial habitat, which may be an impediment to successful establishment of non-native species. Many terrestrial non-native insects are disturbance-adapted and benefit from anthropogenic habitat modification (e.g. urbanization or agriculture) and habitat disturbance which provide conditions that facilitate their establishment and spread (Liebhold et al., 2016; Lozon & MacIsaac, 1997). For example, disturbance-adapted terrestrial invaders are common in the orders Blattodea, Hemiptera and Phthiraptera (Liebhold et al., 2016; Peck & Roth, 1992), which are over-represented orders (see Figure 1). By contrast, freshwater insects typically prefer undisturbed habitats (Rosenberg & Resh, 1993), and, consequently, they are less likely to benefit from anthropogenic habitat alteration. This is partly explained by the lack of tolerance of low oxygen conditions which makes survival and establishment in disturbed, modified or polluted aquatic habitats, where propagules typically arrive, less likely. We found that the primarily aquatic orders Ephemeroptera, Plecoptera and Trichoptera (EPT), most of which are sensitive to deterioration of water quality (Hering et al., 2004; Rosenberg & Resh, 1993; Suhaila & Che Salmah, 2016), are consistently under-represented. By contrast, most established non-native freshwater invertebrates show some tolerance to organic pollutants and low dissolved oxygen (Karatayev et al., 2009). Unlike the EPT, some mosquitoes (Culicidae), hoverflies (Syrphidae) and some other Diptera that are adapted to poor water quality and low oxygen conditions can survive and become established even in small artificial aquatic habitats (Benedict et al., 2007; Derraik, 2005).

The ecological niche of many herbivorous terrestrial invasive insects is determined by the occurrence of their host plants or close relatives, although shifts to novel plants are predictable to some degree (Mech et al., 2019; Pearse & Altermatt, 2013). However, herbivory on vascular plants is considered a less important feeding category in freshwater insects where filter-feeding on phytoplankton or detritus dominate (Allan et al., 2020). Vascular plants are not dominant in most freshwater systems, which probably contributes to the limited number of non-native freshwater insects (Pearse & Altermatt, 2013).

Apart from the Diptera, Coleoptera and Hemiptera also have many representatives that are successful invaders (de Moor, 1992; Liebhold et al., 2021). However, these orders are among the biggest and most diverse insect orders (e.g. Skevington & Dang, 2002; Stork, 2018), and for such diverse groups, it is difficult to determine a single mechanism underpinning the success of invasions. In these cases, an analysis on a scale of families or genera, as conducted for Coleoptera by Liebhold et al. (2021), may more accurately address mechanisms of invasion.

Using either the strict or the broad dataset (based on strict or broad definitions of "aquatic" insect—see methods) did not affect the overall results. The only difference occurred in the significance levels of the comparison between the strict and broad datasets for New Zealand where the difference in the ratios of non-native to native species between freshwater and terrestrial habitats in the strict dataset was marginally nonsignificant. This is probably due to the limited richness range of native freshwater species in New Zealand. As this difference is significant in the broad dataset for New Zealand, and the results were otherwise similar between the strict and broad datasets for Europe and North America, we conclude that the applied definition of freshwater species does not generally affect the overall results. However, the definition of "aquatic species" differs across various sources (compare: Karatayev et al., 2009; Merritt & Cummins, 1996; Merritt et al., 2008), which introduces uncertainty in comparisons among studies and the conclusions that can be drawn. Interestingly, we observed that some non-native freshwater species are herbivores feeding on aquatic host plants (Jäch & Balke, 2008; Mor et al., 2010). As these species can be considered semi-aquatic, we included them in the broad dataset. They included representatives of Coleoptera, Diptera and Lepidoptera, orders which were noticeably more species-rich in the broad dataset, although they remained under-represented.

5 | CONCLUSIONS

To conclude, we provide broad and consistent evidence that invasions of freshwater insect species are relatively rare, in contrast to terrestrial insects which are particularly well represented among invasive species. We show this pattern to be repeated across three world regions (Europe, North America and New Zealand). Two non-exclusive causes are likely to be responsible for this difference: (i) transport pathways facilitating invasions (i.e. international trade) are less effective in moving freshwater insects than terrestrial insects and (ii) characteristics of the life cycles and habitat requirements of freshwater insects predispose them to be less invasive than terrestrial insects. The alternative hypothesis, namely that the differential invasion success is due to freshwater habitats being less invasible than terrestrial habitats, is less plausible, because freshwater habitats are actually highly invaded by other macro-invertebrates (e.g. molluscs and crustaceans) (Karatayev et al., 2009; Ricciardi, 2015). We highlight several more detailed mechanisms that are likely to contribute to the apparent causes (i) and (ii) given above. However, a more thorough understanding of these mechanisms would require more comprehensive experimental approaches and finer taxonomic resolution. Furthermore, understanding these mechanisms can improve predictions of future invaders and their impacts (Pyšek et al., 2012) and provide insights into broader ecological and evolutionary processes (Sax et al., 2007) that play a role in invasions. As we found a surprisingly low overlap among the invasive freshwater species across the regions (with less than 10% of the strictly aquatic invasive species occurring in more than one of our investigated regions), this suggests there is a high potential for further invasions of these "proven invaders." In addition, other species, which have not yet colonized non-native regions, are likely to do so in the future as was shown for other insects and other taxa (Seebens et al., 2017). Future studies should aim at explaining, for example, the invasion patterns observed in diverse groups such as Coleoptera or Diptera. Of considerable importance would also be an improved understanding of the implications of potential differential effects of climate change and other global change drivers on invasions across freshwater and terrestrial habitats.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All relevant data are contained in the manuscript's Supplementary files.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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