

Establishment patterns of non-native insects in New Zealand

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Abstract Insects comprise the majority of non-native animal species established around the world. However, geographic biases in knowledge hamper an overall understanding of biological invasions globally. A dataset of accidentally introduced non-native insect species established in New Zealand was compiled from databases, entomological literature, and examination of specimens in the New Zealand Arthropod Collection. For each non-native species, the first recorded location and first recorded date of detection was obtained. Excluding intentionally introduced species, there are 1477 non-native insect species successfully established in New Zealand across 16 orders, 234 families and 1017 genera. Four orders

(Coleoptera, Hemiptera, Hymenoptera and Diptera) contributed 77.5% of all established insect species. Herbivores represented the largest feeding guild (47.7%), comprised of polyphagous (48.3%) or oligophagous (39.7%) species. The majority of these species originated in the Australasian (36.7%) and Palearctic regions (24.8%). Regression trees, using a binary recursive partitioning approach, found the number of international tourist arrivals, exotic vegetation cover, and regional gross domestic product were the main factors explaining spatial patterns of recently established species. Gross domestic product best explained temporal patterns of establishment over the last century. Our findings demonstrate that broad-scale analyses of non-native species have important applications for border biosecurity by providing insight into the extent of invasions. In New Zealand, the current trajectory indicates fewer non-native species are establishing annually, suggesting biosecurity efforts are being effective at reducing rates of establishment.

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Introduction

Increases in global trade and human travel have facilitated the exchange of a range of species around the world (Liebhold et al. 2013; Seebens et al. 2017). This global exchange of species has brought with it a variety of economic, environmental, and social impacts in recipient regions (Cook et al. 2002; Sax and Gaines 2003; Simberloff et al. 2005). Despite an increased awareness and measures to prevent invasions, the number of species establishing outside their native ranges is still increasing (Hulme 2009; Brouckhoff et al. 2010; Seebens et al. 2017).

Insects comprise the majority of non-native animal species established outside of their native range (Roques 2010; Roques et al. 2016; Yamanaka et al. 2015), and it is likely that the rate of insect invasions will remain steady or perhaps even increase (Meyerson and Reaser 2002; Liebhold et al. 2017). Although non-native terrestrial arthropods are a large part of the invasive species problem, they have received disproportionately less attention than other taxonomic groups (Kenis et al. 2009; Roques 2010). For example, in Europe the largest concentration of research effort has focussed on invasive plant species (44%) (Pyšek et al. 2008). Much of the information across the body of invasion literature has focused on a small number of the most harmful invaders, with 59.7% of 4475 studies addressing a single invasive species (Pyšek et al. 2008). For example, Kenis et al. (2009) showed that within insects, 32% of all papers published on ecological impacts are on just two ant species.

However, broad-scale analyses of non-native insect species are needed to assess which taxonomic or bio-ecological groups are comparatively better invaders (Pyšek et al. 2008). Species inventories allow broad-scale compositional analyses to be undertaken, providing insight into the extent of invasions in different global regions, pathways utilized by invaders, and information on invaded habitats. The combination of non-native species databases and associated broad-scale analyses has been recognised as extremely useful in implementing policy and management regarding biological invasions (Pyšek et al. 2008). Such information can be incorporated into biosecurity efforts and management of introduction pathways between regions. The establishment phase is widely recognised as the most difficult invasion phase for a species to overcome (Lockwood et al. 2005). Establishment may

be determined by a number of factors that vary in space and time. Recent broad-scale analyses of multiple factors have shown the benefits of simultaneously examining a wide range of factors such as disturbance, propagule pressure, biogeography, and species traits, all considered key factors for the establishment of invasive species (Essl et al. 2011; Pyšek et al. 2010).

At present, North America and Europe have historically been considered to have the highest numbers of non-native species and the most studies published compared to other global regions (Pyšek et al. 2008). However, this does not necessarily mean that other regions are less invaded (see Dawson et al. 2017), but rather that there is considerable variation among countries in the scientific effort to detect and describe non-native species. For example, invasive species are severely understudied in much of Asia and Africa whereas Australia and Oceania have disproportionately high numbers of non-native species compared to the number of studies undertaken (Pyšek et al. 2008). Thus, geographic biases hamper an overall understanding of biological invasions and currently limit our knowledge of invasive species distributions globally (Pyšek et al. 2008; Saccaggi et al. 2016).

In New Zealand's phytophagous insect pests cost up to \$880 million per year in direct economic impacts and associated control costs within the agriculture and forestry sectors (Barlow et al. 2002). Despite this, broad-scale spatial or temporal patterns of non-native insect establishment in New Zealand have yet to be analysed. Previous research has focussed instead on smaller taxonomic groups (Teulon and Stufkens 2002; Ward et al. 2006; Brouckhoff et al. 2006) or specific pest groups [e.g., Charles 1993 (for horticulture); Withers 2001 (for insects on eucalypts)].

The main aim of this study was to determine the taxonomic composition of non-native insect species which have established in New Zealand as a result of accidental introductions. Potential factors contributing to the structural composition (e.g., native origin, feeding guild, and host group) were examined. Spatial and temporal patterns of establishment were also determined to examine the relative roles of introduction pressure, disturbance via human activity, biogeographical factors, and search and recording effort, in explaining establishment.

Materials and methods

Species level data capture

A dataset of accidentally introduced non-native insect species established in New Zealand was compiled from several sources: (i) records obtained from the Ministry for Primary Industries' Plant Pest Information Network (from the year 2000 onwards), (ii) the New Zealand Inventory of Biodiversity (Gordon 2010), (iii) the PlantSynz database (Martin 2007), (iv) general entomological databases and literature, and (v) specimens in the New Zealand Arthropod Collection (NZAC). The dataset included non-native species recorded in New Zealand up to 31 December 2014. Searches on non-native species names included all synonyms. Duplicate entries due to changes in taxonomic nomenclature and synonymy were removed, as were species of uncertain establishment. Species that have been deliberately introduced for biocontrol or pollination purposes, or considered to have reached New Zealand by natural dispersal, were also removed.

For each species, the first recorded location and first recorded date in New Zealand were documented. Where such information could not be found from the literature, the earliest collected specimens from populations established in New Zealand were examined at the New Zealand Arthropod Collection (NZAC) (specimens intercepted at the border were not included). Additional information for each species was compiled, including: (i) feeding guild; (ii) host range; and (iii) native biogeographical range of the species. Smaller feeding guilds such as detritivores, pollinators and species feeding on animal products like beeswax were categorised as 'Other'.

Response variables

The total number of species per region, and the total number of species per 5-year interval were used as response variables. These spatial and temporal resolutions were preferable over higher resolutions (i.e., suburbs and cities; months, years, etc.) to allow for a lag between establishment and detection. Spatial and temporal information was collated for each of the 15 regions in mainland New Zealand: Northland, Auckland, Waikato, Bay of Plenty, Gisborne, Hawke's Bay, Taranaki, Manawatu-Wanganui, Wellington, Nelson-

Tasman, Marlborough, WestCoast, Canterbury, Otago, and Southland.

Explanatory variables

Explanatory variables defining each region (spatial analysis; Online Resource 1) and 5 year periods (temporal analysis; Online Resource 2) were split into three categories: introduction pressure, disturbance via human activity, and bio-geographical information (Online Resource 1). For spatial analysis, variables were also obtained to determine if patterns could be explained by sampling and recording effort. Information on explanatory variables was acquired from government departments (see Online Resources 1, 2). Temporal data associated with gross domestic product (GDP) and import values were corrected for inflation using the online inflation calculating tool (http://www.rbnz.govt.nz/monetary_policy/inflation_calculator).

The disparate number of variables for spatial versus temporal analysis is due to the more limited availability of long-term temporal data on core statistics such as human population size and GDP available for temporal analysis over the past century. Temporal response variables were totalled per year for each 5-year block and explanatory variables were averaged (population and temperature) or totalled (GDP and import values) per 5 year block. Spatial analysis was conducted using the total number of species established between 2000 and 2014 and recent explanatory variables (2014), which are assumed to be more representative of the current spatial patterns of establishment (Essl et al. 2011).

Statistical analysis

The relationship between established non-native insect species in New Zealand per order and per family relative to (i) the total number of species worldwide, and (ii) the number of native species in New Zealand was calculated, using log-log linear models. The families used for each analysis included the twenty largest established non-native insect families and a further subset of twenty families selected at random using R. The total number of valid species in each order, or family, globally was used rather than using estimated numbers. Two families of lice, Philopteroidea and Menoponidae, were excluded from

analysis as a global number of species for these families is unknown. The number of native insect species in New Zealand was obtained from the New Zealand Inventory of Biodiversity (Gordon 2010).

Visual analyses of Quantile–Quantile plots and histograms combined with a Shapiro–Wilk test (P value 0.987) indicated explanatory variables were normally distributed. However, many of the spatial variables were highly correlated (Online Resource 3), particularly those representing introduction pressure and disturbance. Similarly, many of the explanatory variables in the temporal analysis were also highly correlated (Online Resource 4). Therefore, for both spatial and temporal analyses, regression trees were used to determine the variables that best explain the patterns of non-native insect establishment.

Regression trees are useful for analyses of ecological datasets (De'ath and Fabricius 2000) with multiple variables that are non-independent and exhibit nonlinear relationships and higher order interactions (Hothorn et al. 2006; Berk 2008). Prior to regression tree analysis, the response variables, being the number of species per region and the number of species per time period, were normalized (square root + 0.5 transformed), then standardized using a mean of zero and a variance of one to account for data with values ranging across three orders of magnitude (Pyšek et al. 2010). To account for the effect of regional area on non-native species numbers, the transformed numbers were regressed against the natural logarithm of the region's area for the spatial analysis. Regression analysis was performed in R using generalized linear models with a log link function for Poisson-distributed data. Pearson's standardized residuals of these models were used as the dependent variables (i.e., describing standardized species numbers adjusted for the effect of region area) in all subsequent spatial analyses (Online Resource 5).

Regression trees were constructed in CART 6.0 by binary recursive partitioning in which the response variable is repeatedly split using the default 'Gini' impurity. The k -fold cross validation method was used for model selection by obtaining the estimates of relative error rates of each tree (Pyšek et al. 2010). The best tree was determined by running 50 sets of tenfold cross-validations on the basis of the minimum-cost rule and on the one-SE rule, which minimise the cross relative error and error within one standard error (SE) of the minimum, respectively (following De'ath and

Fabricius 2000; Witten and Frank 2005). The primary splitter is the variable that best splits the data at the node while minimizing the error of the subsequent nodes (Van Engelsdorp et al. 2010). The quality of each split is represented by its improvement value (a higher value represents better quality), while the variable's importance reflects the variable's role as a primary splitter and as a surrogate to other primary splitters and therefore its overall contribution to predicting the response variable.

All analyses were performed in the R software environment. Details on specific R packages used for each analysis are provided in Online Resource 6.

Results

Taxonomic composition

Based on the inventory we compiled, there are 1477 non-native insect species that have been accidentally introduced to New Zealand and successfully established. This non-native insect fauna is comprised of 16 orders, 234 families, and 1017 genera. Four orders (Coleoptera, Hemiptera, Hymenoptera and Diptera) contributed 1145 species which represents more than three quarters (77.5%) of all established insects, with beetles (Coleoptera) being the largest (412 species or 27.9%), followed by Hemiptera and Hymenoptera (Fig. 1). The families Aphididae (Hemiptera) and Staphylinidae (Coleoptera) were the top two families (Fig. 1). Success rates regarding data capture varied between orders (Online Resource 7), but in general were high (median values > 77% for all variables).

The number of non-native insect species per order in New Zealand was significantly correlated with the total number of species in the order world-wide (P value < 0.001) (Fig. 2). The model explains 69% of the data and indicates a strong correlation between these variables ($r^2 = 0.86$) and a Bonferroni test failed to detect any significant outliers (Bonferroni $P > 0.05$). The number of non-native insect species per family was not significantly correlated with the total number of species per family world-wide but there is a notable linear trend (P value = 0.053) between the number of non-native species in each family in New Zealand and the size of each family globally (Fig. 2). The model explains 92% of the data and indicates a weak linear correlation between

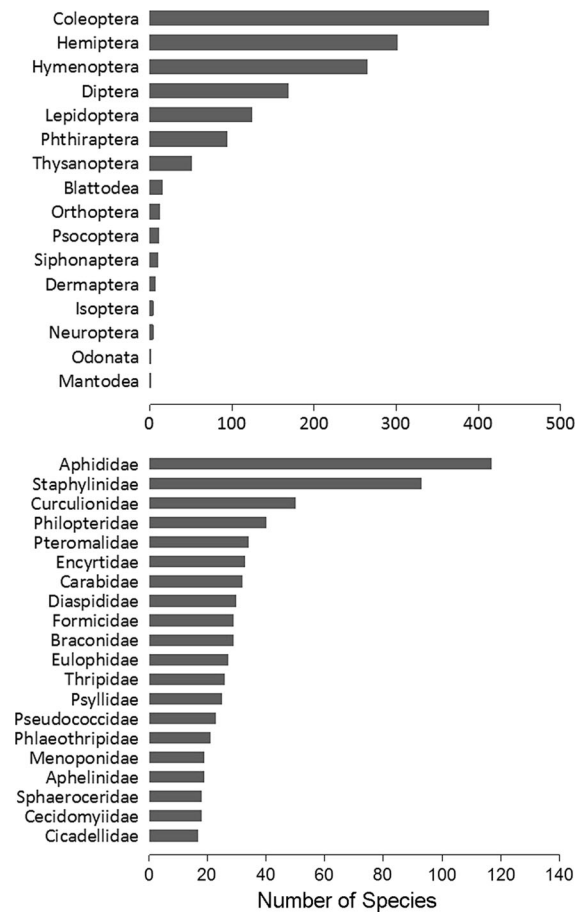
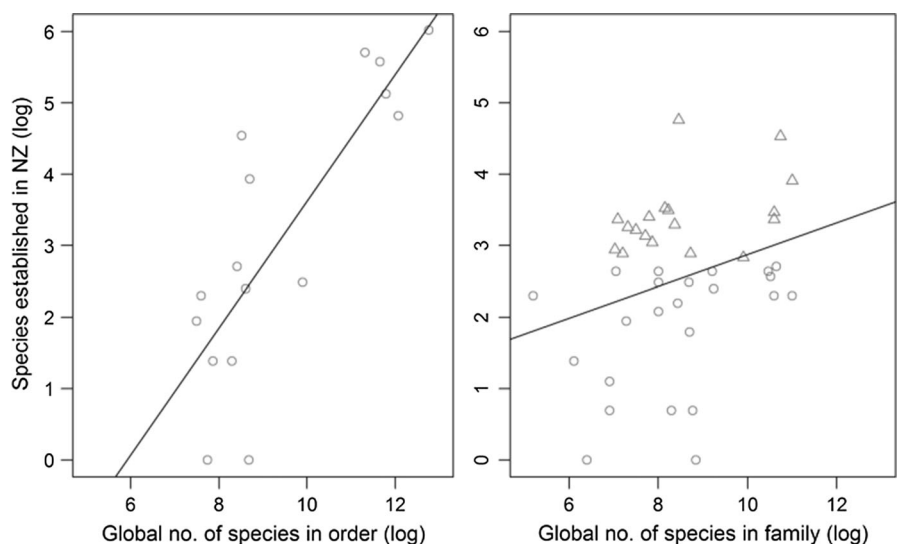


Fig. 1 Taxonomic composition of the total number of non-native insect species established in New Zealand by order (left) and the top 20 families (right)

Fig. 2 Comparison of the number of established non-native insect species in New Zealand by order (left), and family (right), as a function of the total number of species globally. The solid line is the regression slope fitted to the data (order: $r^2 = 0.86$, P value < 0.001 , family: $R^2 = 0.24$, P value $= 0.053$). The twenty families with the most established species in New Zealand, excluding Philopteridae and Menoponidae are indicated by triangles



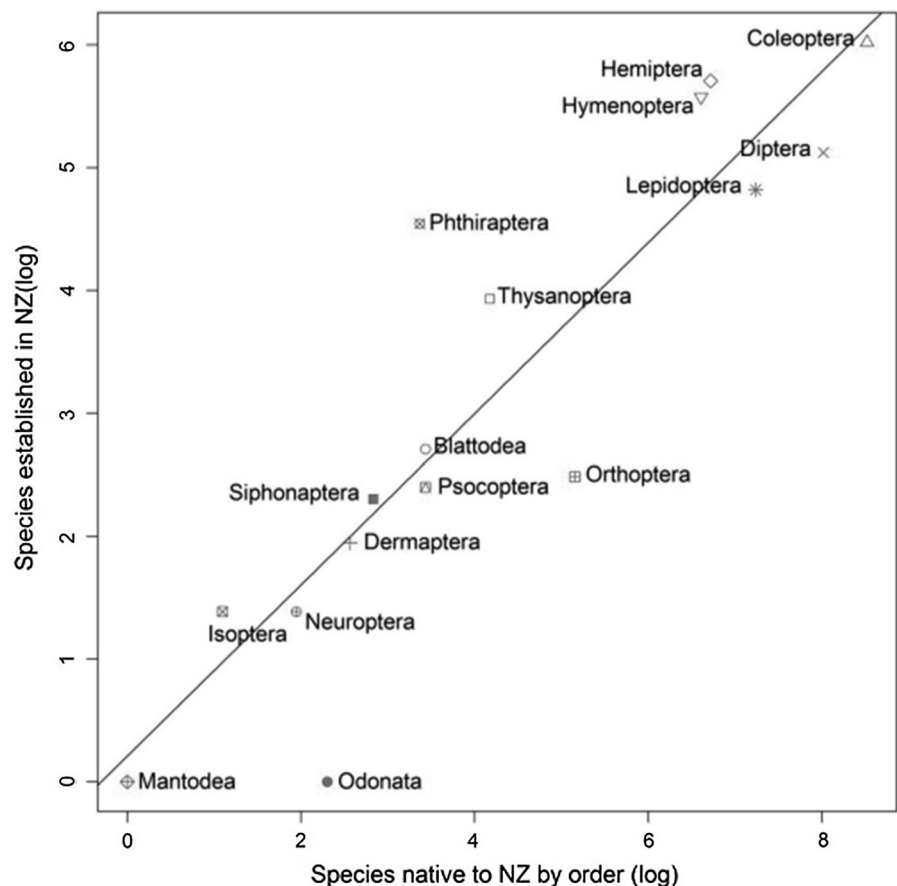
variables ($r^2 = 0.24$). There is also a strong correlation between the number of non-native species and the number of native species within an order (P value < 0.001 , $r^2 = 0.79$) with the model explaining 80% of the data (Fig. 3). There are more native species in Orthoptera and Odonata, but notably more non-native species in Hemiptera, Phthiraptera and Hymenoptera, although these are not significant outliers (Bonferroni $P > 0.05$).

Origins and feeding guilds

Non-native insect species established in New Zealand primarily originated from the Australasian (36.7%) and Palearctic regions (24.8%) (Fig. 4, Online Resource 8). The primary origin for the majority of orders is Australasia, including some of the larger orders such as Hemiptera, Coleoptera and Hymenoptera. A similar number of Australasian and Palearctic species were recorded in New Zealand until 1915, but since then, species from Australasia rapidly increased and became the largest source of non-native species in New Zealand (Fig. 5).

The non-native insect feeding guild primarily consists of herbivores (47.7%) followed by parasitoids (13.2%) and predators (10.7%) (Fig. 4). Overall, 11.9% of species are monophagous (140 species) but the majority of species exhibit wider host ranges with 39.7% being oligophagous (466 species) and 48.3% being polyphagous (567 species). Of the oligophagous

Fig. 3 Numbers of non-native insect species in each order relative to the number of native species in each Order. The line represents the linear correlation coefficient ($r^2 = 0.79$). Point symbols represent the order of the species group



species, 32% can be further classified as genera-oligophagous (i.e. oligophagous at the genus level) and only feed on certain genera, while 51.1% are family-oligophagous and 16.8% are order-oligophagous. Many of the species exhibiting host specificity are parasitoids (79.7%), parasites (8.6%), or predators (7.3%).

Spatial patterns of establishment

Between 2000 and 2014, a total of 103 non-native insect species were first recorded in New Zealand. The number of international tourists visiting a region, and the percentage of non-native vegetation area in the region, best explained the spatial pattern of establishment (Fig. 6). The best regression tree explained 78% of the data (R^2 lean = 0.781) and had a cross validation error of 0.585 indicating the model has predictive capability for the spatial distribution of established non-native insects. The number of tourists

per year explained 53% of the variance. Regions which received higher numbers of tourists per year received 85.4% non-native insect species (terminal node 3). Regions which received less tourists were subsequently split by the percentage of exotic vegetation cover which explained 15% of the variance.

Regional gross domestic product, the number of professional science jobs, and tourist expenditure, and were equally competing variables as the primary splitter (Online Resource 9). Running the analysis without the number of tourists produced a tree with only one splitter, regional GDP (millions \$8840.5) with a cross validation error of 0.907, indicating while this is still useful for prediction it is not as effective as the primary tree.

Temporal patterns of establishment

Overall the number of newly recorded species steadily increases from 1769 and although pulses of

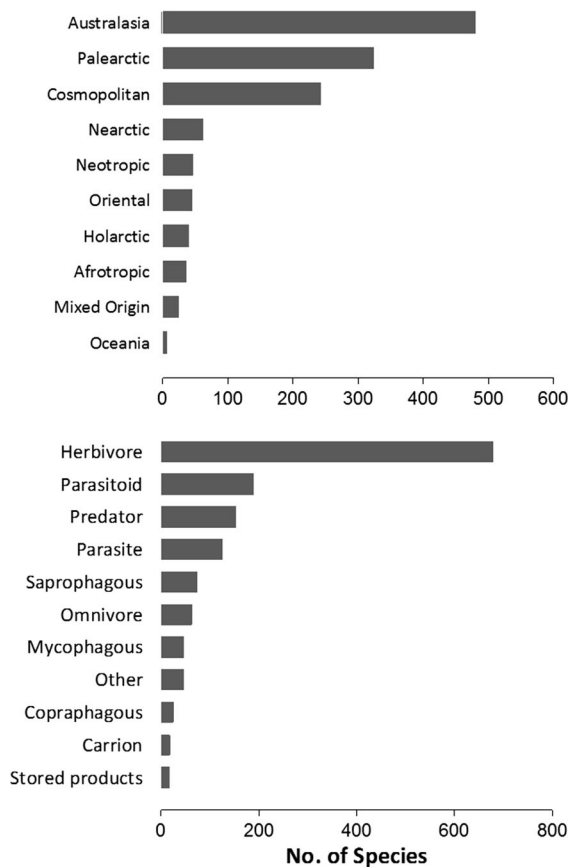


Fig. 4 Total number of non-native insect species established in New Zealand by biogeographic origin (top) and feeding guild (bottom)

establishment are evident during 1920–1925 and 1975–1980, from the 1970s first records slowly begin to decrease (Fig. 7). The relationship between the number of species recorded and time is non-stationary (test for a quadratic P value < 0.001). A general linear model with an applied polynomial quadratic indicates this relationship is non-linear, explaining 99.8% of the variation (P value < 0.001 , $r^2 = 0.99$), with a negative trajectory since the 1975–1980 period (Fig. 8).

Gross domestic product was the best variable predicting the temporal pattern of establishment (Fig. 9). The best regression tree explained 66% of the data (R^2 lean = 0.657) and had a cross validation error of 0.487 indicating the model has a good predictive capability of the temporal distribution of non-native species. Gross domestic product is both the primary and secondary splitter, explaining 94% of the variance overall. The value of imports is the only

notable competitor for the root node splitter (Online Resource 10). Removing GDP as a main predictive variable produces a similar tree with value of imports representing both the primary and secondary splitter, but explains less of the data than the initial temporal regression tree (R^2 lean = 0.497) and with a higher cross validation error (0.561).

Discussion

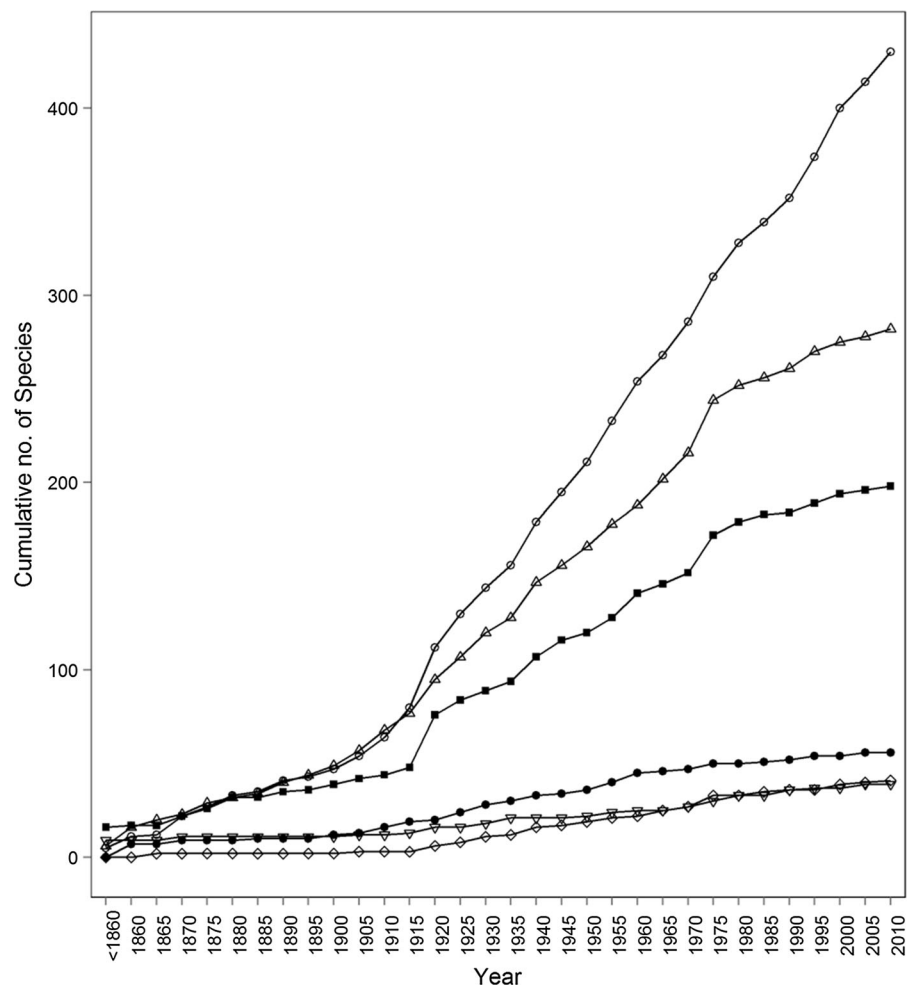
Non-native insects in New Zealand

We recorded 1477 accidentally introduced non-native insect species present in New Zealand. The relative size of non-native insect taxonomic groups in New Zealand is largely a function of their global size. For example, the number of non-native insect species per order in New Zealand were significantly correlated with the total number of species per order world-wide. This relationship was not as strong at the family level, but there was a strong non-linear relationship in which non-native Aphididae and Formicidae were notably over-represented compared to the number of native species.

The frequency with which different groups of insects have invaded can be expected to be associated with their levels of invasiveness and their ability to become associated with certain human mediated pathways of dispersal (Liebhold et al. 2016). The order Hemiptera is particularly over-represented in New Zealand compared to native species, and follows findings by Liebhold et al. (2016), whereby the over-representation of Hemiptera in non-native insect compositions is evident across multiple countries. This relationship is, by far, the most prevalent in the Aphididae, exhibiting a 39:4 ratio (non-native to native species) in New Zealand. Aphids are considered taxonomically underrepresented in the tropics and in the southern hemisphere, and this is particularly evident in the depauperate New Zealand native aphid fauna (Teulon and Stufkens 2002). A similar pattern occurs with ants, where there is a depauperate New Zealand native ant fauna, and strong propagule pressure of exotic species via trade (Ward et al. 2006).

Internationally, the introduction of a number of non-native species can often be predicted from their association with specific commodities (Hulme et al. 2008). Insects are often transported on commodities

Fig. 5 Cumulative number of non-native insect species established over time by native origin. (Open circles—Australasia, open triangles—Palearctic, closed squares—Cosmopolitan, closed circles—Nearctic, open diamonds—Neotropic, downward open triangles—Oriental)



such as nursery stock, cut flowers, fresh food, seeds, wood packing material, logs, and lumber (Brockerhoff et al. 2006; Haack 2006). While there are a number of important pathways utilized by non-native insects species, perhaps the most significant driver of global biological invasions is the importation of live plant material (Kenis et al. 2007; Liebhold et al. 2012, 2013). Overall, the large proportion of phytophagous non-native insects established in New Zealand indicates that imported whole plants and cuttings are highly influential in shaping the spatial distribution and composition of non-native insects.

There is also a taxonomic bias associated with ornamental plant trade of commodity, in particular, aphids and scale insects are often carried inconspicuously into new regions with their host plant (Kenis et al. 2007; Roques et al. 2009). This is reflected in the high numbers of species in both families established in

New Zealand, where many aphid species established in New Zealand are thought to have arrived on plant material during early European colonisation (Teulon and Stufkens 2002). Equally, the importation of crop species may be responsible for the relatively high number of non-native thrips (Thysanoptera) in New Zealand, which are predominantly phytophagous.

The importation of plants may also bring natural enemies that are associated with phytophagous insects, that is, predators and parasitoids. Natural enemies could easily be accidentally introduced when both the host plant and host insect are imported (Ward and Edney-Browne 2015). For example, parasitoid families such as Aphelinidae, Encyrtidae, and Eulophidae (Hymenoptera), which are often associated with plant-feeding hosts (namely Hemiptera), are particularly speciose as invaders in both New Zealand and Europe (Ward and Edney-Browne 2015). Records

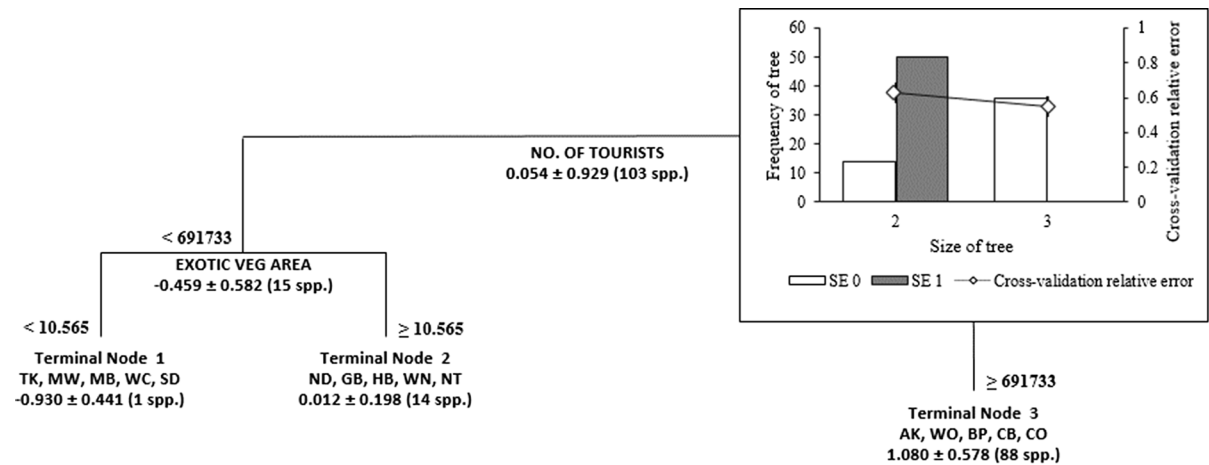
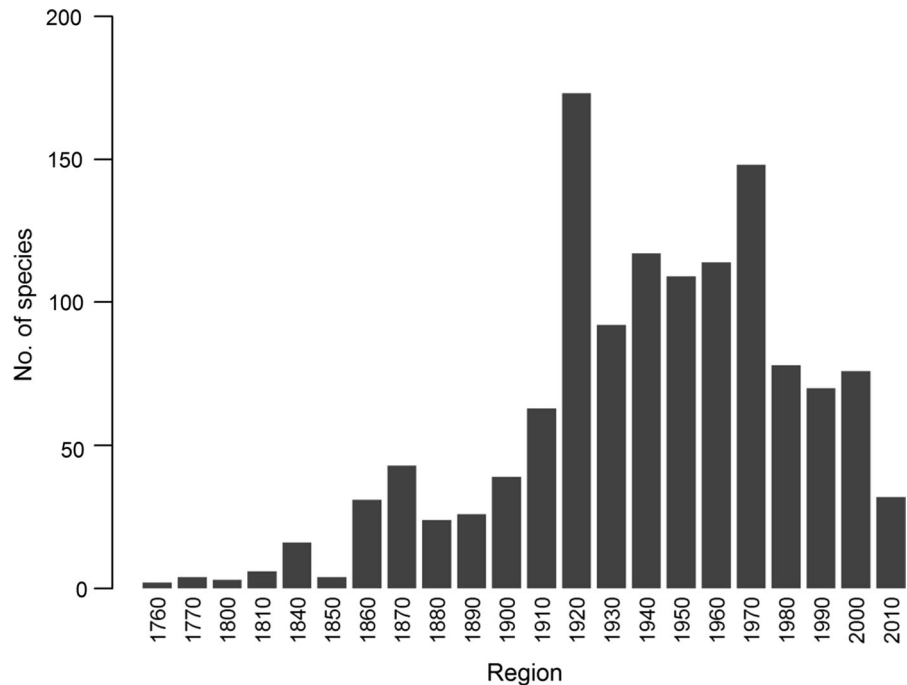


Fig. 6 Regression tree analysis explaining the spatial distribution of non-native insect establishment in New Zealand. Each node of the tree is described by the splitting variable, the splitting criteria, mean \pm standard deviation for the number of first recorded locations of non-native insect species, and the number of sample (i.e. species) at that node in brackets. Splits are the number of tourists (actual count), and exotic vegetation

area (%). (Inset) Bar charts are the numbers of the optimal trees of each size (frequency of tree) selected from a series of 50 cross-validations based on the minimum cost tree, which minimizes the cross-validated relative error (white, SE rule 0), and 50 cross-validations based on the one-SE rule (grey, SE rule 1), which minimizes the cross-validated relative error within one SE of the minimum

Fig. 7 Number of non-native insect species first recorded in New Zealand per 10 year period



show these families have a very low proportion of being intercepted at the New Zealand border but contribute a high proportion of established species (Ward and Edney-Browne 2015). This suggests that these parasitoid groups are less often discovered

during border inspections, possibly because they are relatively small and have cryptic behaviours, including being inside their hosts (Ward and Edney-Browne 2015).

Fig. 8 The relationship between the number of non-native insect species established in New Zealand over time (per 5 year period). The solid (blue) line represents a 0.75 lowess smoother and the dotted (red) lines indicate 95% confidence intervals

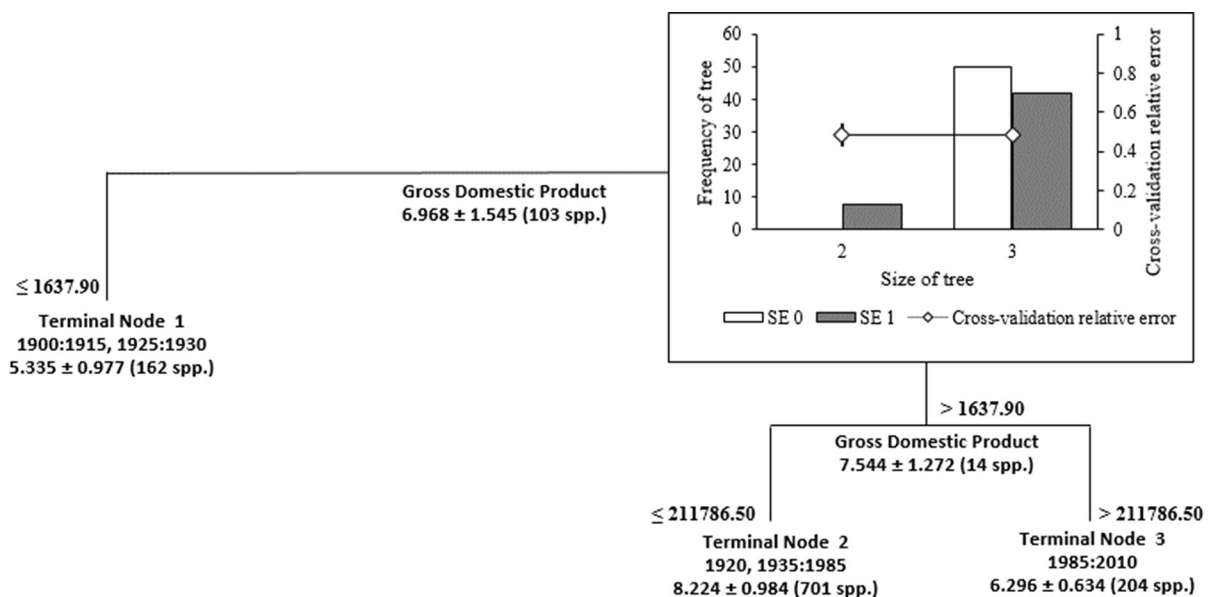
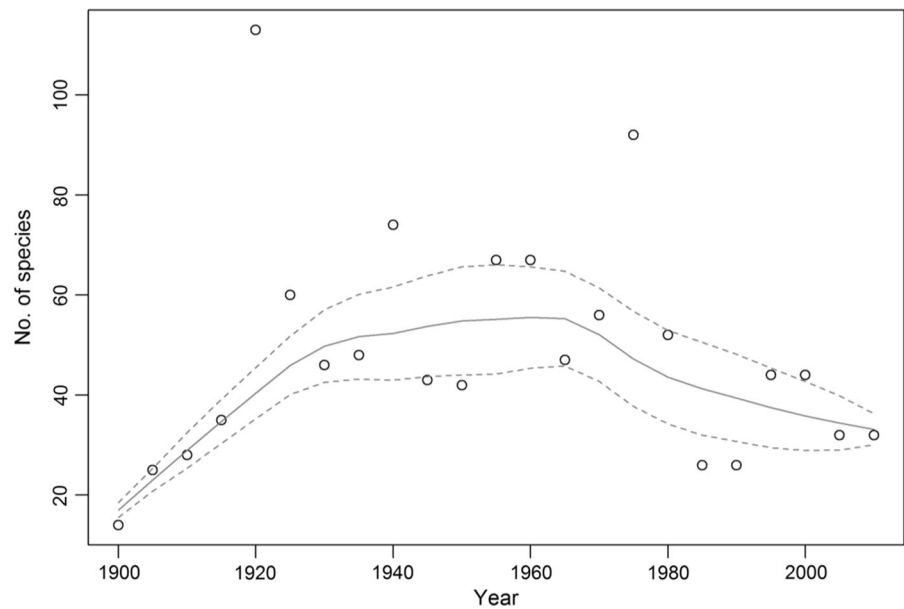


Fig. 9 Regression tree analysis explaining the temporal distribution of non-native insect establishment in New Zealand. Each node of the tree is described by the splitting variable, the splitting criteria, mean \pm standard deviation for the number of first recorded locations of non-native insect species and the number of sample (i.e. species) at that node in brackets. Split is gross domestic product unit (NZ\$ millions). (Inset) Bar charts

are the numbers of the optimal trees of each size (frequency of tree) selected from a series of 50 cross-validations based on the minimum cost tree, which minimizes the cross-validated relative error (white, SE rule 0), and 50 cross-validations based on the one-SE rule (grey, SE rule 1), which minimizes the cross-validated relative error within one SE of the minimum

Notable spatial and temporal patterns

Variables associated with propagule pressure (the number of international tourists), and disturbance

(exotic vegetation cover) were identified as the primary and secondary factors explaining spatial patterns of non-native insect establishment. However, regional GDP was the primary explanatory variable

when the number of international tourists was excluded. Tourists are not considered to be a dominant vector of invasive insects, and the apparent role of the number of tourist arrivals is probably more an indication economic activity and transport hubs that are also receive most imports. Consequently, we suggest that regional GDP is a more meaningful explanatory variable for this dataset. Our knowledge of invasion pathways indicate that trade and imported commodities are more meaningful as predictors than the number of tourists (Hulme 2009; Pyšek et al. 2010; Liebhold et al. 2016; Saccaggi et al. 2016).

In terms of temporal patterns, gross domestic product was the most important variable explaining non-native insect establishment in New Zealand. However, the value of imported commodities was also a strong explanatory variable in the regression tree analysis and was correlated with gross domestic product, indicating its role in the establishment process. These results reflect those from Pyšek et al. (2010) who used regression trees and variance partitioning to examine biological invasions across Europe. Human population and cumulative wealth were the key drivers across multiple non-native taxa (Pyšek et al. 2010). For both spatial and temporal datasets, the results show the complex nature of disentangling the multiple variables which are involved in biological invasions (Pyšek et al. 2010).

The relative unimportance of biogeographical and climatic factors in explaining spatial patterns of non-native insect establishment in New Zealand is also of interest. Climatic and biogeographical variables such as temperature and vegetation cover were of low significance. Again, this does not mean that these factors have no role in the establishment of non-native insects; they may be influential at different scales and at different times during the invasion process. However, the relative unimportance of these factors is in keeping with several recent analyses where socio-economic conditions have been positively associated with regional numbers of species across multiple taxa and are more important in explaining variation in invasion patterns than ecological factors (Pyšek et al. 2010; Essl et al. 2011). It implies that the influence of non-socioeconomic variables may be over-estimated in analyses of factors determining distributions of non-native species. Consequently, analyses must consider both sets of variables (biogeographical and socioeconomic) when analysing data to ensure predictions

made on the distribution of non-native species are robust.

The first record of a species may not reflect the exact time that this species established in its non-native range (Costello and Solow 2003; Crooks 2005). We acknowledge there can be considerable time lags between the date of actual establishment and the date when a species is first detected (Crooks 2005), thus potentially affecting the relationship between response and explanatory variables. However, the frequency distribution of such time lags is largely unknown, and we suggest it is inaccurate to ubiquitously apply long lags across all species. The link between establishment and detection of a species may also be context dependent. For example, the detection for large, and/or conspicuous species may be more analogous with their initial establishment, than for small, cryptic insect species. There may also be a time-period dependency because, historically, little, if any surveillance activities were in place. Thus, time lags between establishment and detection could have been longer in the past. In this study, we used 5-year time intervals to help smooth annual idiosyncrasies in both response and explanatory variables. However, we argue that more research is needed to explore relationships between establishment and detection.

Are border biosecurity efforts working?

A recent global analysis showed no sign in the saturation of non-native species, with most taxa showing increases in the rate of first records over time (Seebens et al. 2017). However, an exception in this global dataset was for vascular plant species in New Zealand, where rates of first records have dropped because of increased biosecurity measures (Seebens et al. 2017).

Our results strongly indicate that the rate of non-native insect species establishing in New Zealand has also been slowly decreasing. This would strongly indicate that New Zealand's biosecurity efforts have been successful in reducing the establishment rate of non-native insects. This overall decline is in agreement with studies of specific non-native insect groups in New Zealand. For example, approximately one aphid species had established every year from 1860–1990, but since 2002, aphid species are establishing at half that rate, on average one aphid species

establishing every 2 years (Teulon and Stufkens 2002).

As a relatively small island nation with well-defined borders and advanced biosecurity systems, New Zealand may have a natural advantage compared with most countries in other global regions regarding the implementation of effective measures preventing the establishment of unwanted organisms, which may explain, in part, the current decline in non-native insects establishing in New Zealand. Furthermore, New Zealand has the highest national-level biosecurity expenditures in the world relative to GDP, spending 0.076% of GDP, compared to other high investors; Australia (0.007% of GDP) and the US and UK (0.001–0.002% of GDP) (Dalmazzone and Giaccaria 2014). This reflects the importance placed on biosecurity in New Zealand, with policies evolving a broader awareness of multiple social, economic and ecological objectives (Jay et al. 2003; Goldson 2011).

Conclusions

It is evident that human-mediated dispersal has introduced a large number of species into New Zealand which were unlikely to have established otherwise. The over-representation of some insect Orders is likely due to the possession of life history traits which aid in overcoming barriers associated with establishment and through the association with particular introduction pathways (e.g., fresh produce and live plant imports). Patterns of species establishment were statistically explained at a high level, with low cross validations, indicating good predictive ability. We advocate for the continued broad-scale analyses of temporal and spatial patterns of non-native species establishments to improve our understanding of where, and when, species are establishing. Such information can ultimately be incorporated into the management and policy of preventing invasions of unwanted organisms.

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Data accessibility The list of species and associated data is publicly available (<https://doi.org/10.7931/J20K26HK>) Edney-Browne E, Brockerhoff EG, Ward DF. First records of the establishment of exotic insects in New Zealand <https://doi.org/10.7931/j20k26hk>.

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