The great escape: patterns of enemy release are not explained by time, space, or climate

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Abstract

When a plant is introduced to a new ecosystem it may escape from some of its coevolved herbivores. Reduced herbivore damage, and the ability of introduced plants to allocate resources from defence to growth and reproduction can increase the success of introduced species. This mechanism is known as enemy release and is known to occur in some species and situations, but not in others. Understanding the conditions under which enemy release is most likely to occur is important, as this will help us to identify which species and habitats may be most at risk of invasion. We compared in-situ measurements of herbivory on 16 plant species at 12 locations within their native European and introduced Australian ranges to quantify their level of enemy release and understand the relationship between enemy release and time, space, and climate. Overall, plants experienced approximately seven times more herbivore damage in their native range than in their introduced range. We found no evidence that enemy release was related to time since introduction, introduced range size, temperature, precipitation, humidity, or elevation. From here, we can explore whether traits such as leaf defences, or phylogenetic relatedness to neighbouring plants, are stronger indicators of enemy release across species.

Introduction

Herbivores are the bane of almost any plant's existence and can severely limit individual fitness and population growth (Crawley, 1989; DeWalt et al., 2004; Marquis, 1984; Morris et al., 2007; Mothershead & Marquis, 2000). In most natural ecosystems, plants and their herbivores have co-evolved over millions of years, with plants gaining protective traits to reduce damage, and herbivores adapting to overcome plant defences (Dawkins & Krebs, 1979; Mithöfer & Boland, 2012; War et al., 2012). As such, interactions between plants and herbivores can become unique to the ecosystems they naturally inhabit (Thompson, 2005). So, when a plant is introduced to a new ecosystem it may be freed from the constraints of the herbivores that once restricted it in its native range (Keane & Crawley, 2002). This mechanism is referred to as enemy release (Blossey & Nötzold, 1995; Colautti et al., 2004; Crawley, 1987; Keane & Crawley, 2002).

Escaping from the herbivores that co-evolved with a plant species in its native range can be a major contributor to a species' success in an introduced range (Keane & Crawley, 2002). However, studies suggest that only about half of introduced species actually experience enemy release (Colautti et al., 2004; Hawkes, 2007; Jeschke et al., 2012; Keane & Crawley, 2002; Liu & Stiling, 2006; Pyšek et al., 2008). Most of our understanding of enemy release tends to focus on case studies of one or a small number of species, with relatively few examples of field comparisons across multiple species and locations (Hierro et al., 2005; Meijer et al., 2016; Roy et al., 2011). The limited taxonomic scope of most previous studies means that we have no empirical evidence about the spatial, temporal, and climatic circumstances that might allow us to predict whether a particular introduced plant species is likely to experience enemy release. Our study addresses this knowledge gap using a biogeographical approach to quantify the factors contributing to successful enemy release in a broad range of plant species in multiple, diverse locations within their native and introduced ranges.

We first ask whether the amount of herbivore damage our study species receive differs between their native and introduced ranges. Answering this question allows us to understand which plants are experiencing enemy release and the magnitude to which they are affected, allowing us to explore further questions on the factors contributing to enemy release. We hypothesise that plants in the introduced range will suffer less herbivore damage overall, as they are more likely to have escaped their enemies according to the enemy release hypothesis (Blossey & Nötzold, 1995; Keane & Crawley, 2002).

We then test a range of hypotheses that aim to better predict when and where enemy release is most likely to occur.

Our first prediction is that the magnitude of enemy release plant species experience will decrease with time since introduction. Native herbivores, especially those with specialised interactions, usually prefer to feed from the native plants they have co-evolved with, and can struggle to tolerate invasives (Rodríguez et al., 2019; but see Morrison & Hay, 2011). Yet as time passes, some introduced species may eventually accumulate “enemies” as herbivores switch feeding between native and introduced hosts, as shown by Rodríguez et al. (2019) in a case study of *Acacia dealbata* and *Carpobrotus edulis* invasions on the Iberian peninsula. However, a study, spanning 35 species, showed no effect of time since introduction in relation to a plant’s degree of herbivory (Carpenter & Cappuccino, 2005). A meta-analysis found that enemy release is higher in species that were introduced more recently (< 50 years ago) and lower in plants that had established earlier (50-200 years ago), with herbivory levels similar to conspecifics in their native range (Hawkes, 2007). Our study extends and complements these previous findings and is the first to account for variation in enemy release across multiple species and sites within the native and introduced ranges.

Subsequently, we ask whether the degree to which species experience enemy release is negatively correlated with their introduced range size. According to the species-area relationship, larger areas can foster a greater diversity of organisms in comparison to smaller fragments and studies have shown that arthropod diversity is best predicted by the range size of host plants (Colautti et al., 2004; Lomolino, 2001). However, no studies have previously tested whether a relationship between range size and enemy release exists. As plant species with smaller range sizes are less likely to encounter and accumulate a diversity of herbivores than those with larger range sizes, we predict that species with smaller introduced range sizes are more likely to experience stronger enemy release.

Finally, we ask whether enemy release is correlated with the climate or elevation of the introduced sites they occupy. As ectotherms, invertebrate herbivores' metabolism and rate of consumption are regulated by their external environment, and rise with increasing temperature (Brown et al., 2004; Hillebrand et al., 2009; Kozlov et al., 2015). Patterns with water availability are less clear, with some evidence that leaf damage increases with precipitation (Ebeling et al., 2022; Njovu et al., 2019), but other evidence that relative humidity is negatively correlated with herbivory (Reynoso & Linera, 2007). The negative relationship with relative humidity could be explained by humidity's inversely proportional relationship to temperature, as air becomes drier as temperature increases, which in turn, increases the rate of herbivory. Invertebrate presence and leaf damage are also lower at higher altitudes, possibly due to lower temperatures and resource availability (Moreira et al., 2018; Reynolds & Crossley, 1997). We therefore hypothesise that enemy release will be negatively correlated with temperature and precipitation, and positively correlated with humidity and elevation.

In summary, we predict:

1. Overall, plants will experience more herbivore damage in their native range than in their introduced range.
2. Enemy release will decrease with time since introduction.
3. Enemy release will decrease with the size of the invaded range.
4. Enemy release will decrease with increasing temperature and precipitation.
5. Enemy release will increase with humidity and elevation.

Materials and Methods

Data collection

To determine whether introduced vascular plant species are experiencing enemy release in Australia, we measured leaf damage at 12 separate sites within the native and introduced ranges of 16 plant species (Fig. 1). We incorporated data from ecologically diverse locations (i.e., the dry, warm mountainous region of northern Madrid to the cool, damp meadows of the English midlands) within each range, to better reflect the variation in herbivory that plants can receive across different habitats/populations. We confirmed each species' status as either native to Europe, or introduced to Australia, from the literature.

We chose our target species based on three main criteria whereby each species must:

1) Have a widespread presence in both Europe (as a native plant) and south-eastern Australia (as an introduced plant).

2) Not actively be managed by biocontrol agents in Australia (because biocontrol agents work by countering enemy release).

This yielded a list of over 25 plant species eligible for inclusion in our study. However, despite our best efforts in the field, some species could not be located and measured at least once in the native range and once in the introduced range. Our third criteria was thus that species were measured in at least one site across both ranges (native and introduced). Our final dataset includes measurements from 16 herbaceous plant species (15 eudicots and 1 monocot) belonging to 14 families and 11 orders (Appendix S1). Of these species, six (*Convolvulus arvensis*, *Hypericum perforatum*, *Leucanthemum vulgare*, *Parietaria judaica*, *Rumex acetosella*, and *Verbascum thapsus*) are listed as invasive by Weeds Australia (https://weeds.org.au/).

When choosing our study sites, we prioritised maximising the latitudinal range and landscape diversity in each range. Target species presence was also factored into site choice as we preferred to visit places that would increase our sampling potential. We used online databases such as the Global Biodiversity Information Facility (gbif.org) and the Atlas of Living Australia (ala.org.au) to assess target species presence prior to choosing our site locations. Not all study species were present at each site (i.e., city or region where sampling took place) (Appendix S2).

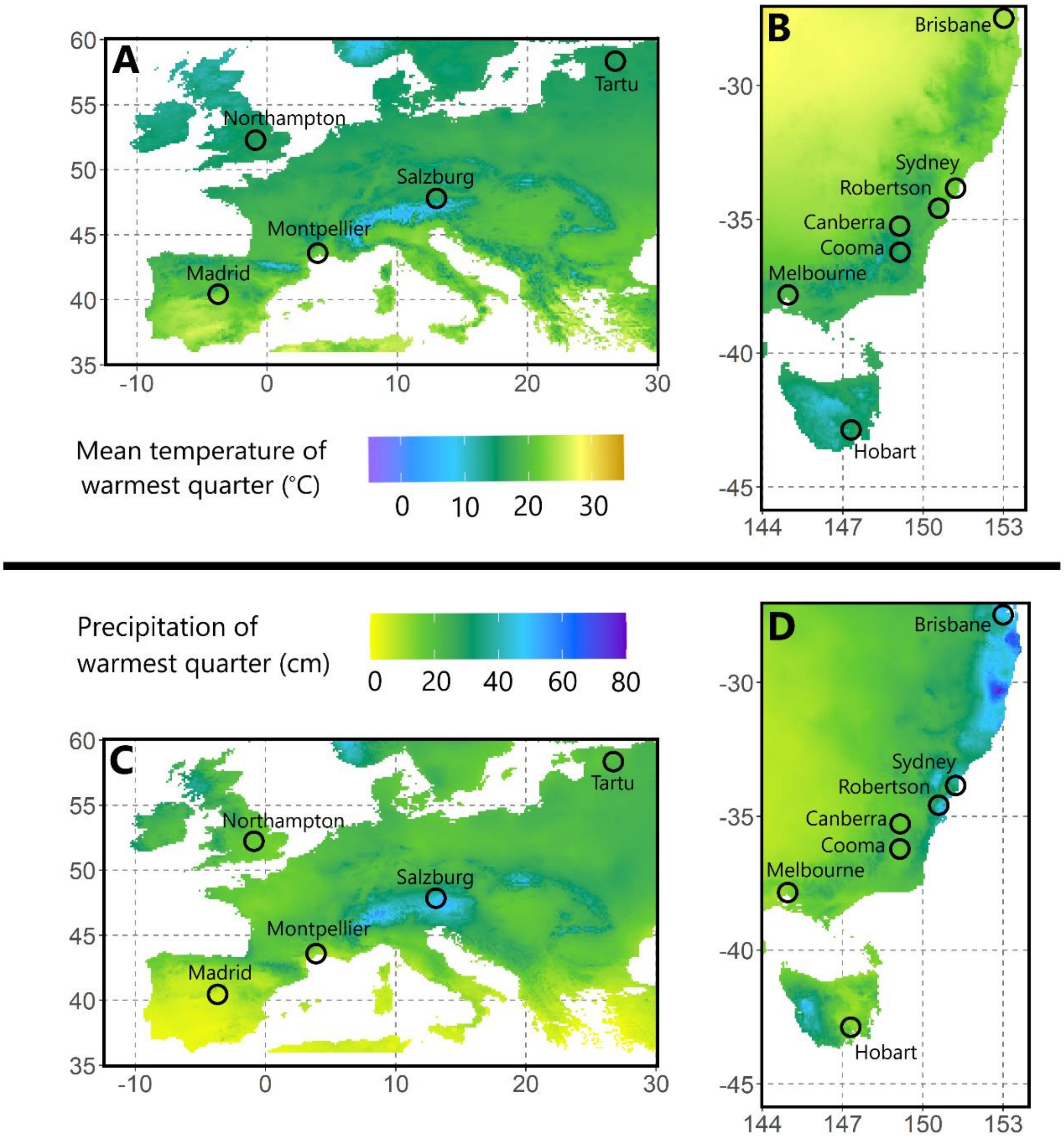

Figure 1. Maps of sampling sites in (a, c) Europe (native range) and (b, d) Australia (introduced range). Sites in Europe include Madrid (Spain), Montpellier (France), Salzburg (Austria), Northampton (United Kingdom) and Tartu (Estonia). Sites in Australia include Hobart (Tasmania), Melbourne (Victoria), Cooma (New South Wales), Canberra (Australian Capital Territory), Robertson (New South Wales), Sydney (New South Wales) and Brisbane (Queensland). Maps are shaded according to (a, b) mean temperature of the warmest quarter and (c, d) total precipitation of the warmest quarter from WorldClim version 2.1 climate data for 1970-2000 (Fick & Hijmans, 2017).

At each site, we aimed to measure foliar herbivory on ten leaves of at least twelve individuals per species. Individuals were chosen by selecting the first twelve plants of each target species that we encountered at each site. We distinguished individuals by ensuring they were spaced at least 2 m apart, with clonally spreading species requiring at least 5 m distance. We began measuring from the first fully expanded leaf on the highest branch and continued towards the base of the stem. Where there were fewer than 10 leaves on a branch, we continued to measure on the branch/es directly below until ten measurements were recorded. Where there were fewer than 10 leaves per individual, we compensated by measuring more individuals until we reached a similar number of measured leaves. Species with compound leaves (e.g. *Trifolium repens* and *Lotus corniculatus*) had their herbivory measured per leaflet (ten leaflets of twelve individuals) in a clockwise direction from the petiole. The herbivory examined in this study is ectophagy and does not consider the identity of the herbivores or their functional interactions.

Herbivory measurements were calculated as a percentage of removed or damaged leaf tissue, including the lamina and petiole. Visual estimates were used to assess herbivory on a scale of 0-100%, by mentally dividing the leaf into four equal quadrants and visualising the damage all together in one section (Harvey et al., 2013). We chose to estimate leaf damage visually as it only takes ~10 seconds to measure each leaf, allowing us to notably increase our sample size and perform all observations in the field (Getman-Pickering et al., 2020; Schaffer et al., 1997; Xirocostas et al., 2022). All visual estimates of herbivory were conducted by the lead author (ZAX) after being trained to measure herbivory on leaf images with known damage. Assessor accuracy was assessed twice in the field (once in Europe and once in Australia) by visually estimating a subsample of leaves and then digitally analysing their amount of leaf damage using ImageJ. All visually assessed estimates were within 1% accuracy of the digital measurements. Field observations took place in the peak growing seasons of 2019, from May – July in Europe and between September – November in Australia.

To assess whether enemy release is related to plant species' time since introduction we compiled data on species' year of introduction to Australia from the literature. The literature reports initial occurrences of species introductions (or estimates thereof) to the continent of Australia but does not account for multiple introductions of a species to varying regions. However, as we are testing this relationship on the macro-scale, coarser records are sufficient, as any pattern arising from data with greater uncertainty would only strengthen its support for a relationship. For each target species we searched two online databases, the Atlas of Living Australia (ala.org.au) and the Web of Science, to determine the year of their earliest known occurrence in Australia. For the Atlas of Living Australia, we simply searched each species by scientific name to access their earliest recorded occurrence in Australia. For the Web of Science, we used keywords such as "year" "introduc*" and "Australia" accompanied by scientific name. We calculated time since introduction by subtracting species' year of introduction from the year herbivory observations took place (2019).

To understand whether enemy release is associated with plant species' introduced range size we gathered range size data from the Atlas of Living Australia's spatial portal (spatial.ala.org.au; accessed 22nd of June 2021; Appendix S3). We chose "area of occupancy" as a metric to assess our species' geographic spread. We added each species, separately, into the spatial portal (restricting records to only those that were spatially valid and within Australia) and used the "calculate AOO and EOO" function (with a grid resolution of 0.05 decimal degrees and alpha hull of 2) to attain the area of occupancy (km^2), which we hereby refer to as range size for introduced populations.

To understand whether enemy release is associated with climate and elevation we downloaded data from:

1. WorldClim v2.1 at 2.5 minute resolution (Fick & Hijmans, 2017) for mean annual temperature, annual precipitation, mean temperature of the warmest quarter, and precipitation of the warmest quarter. Mean annual temperature and annual precipitation were chosen as they are meaningful predictors for plant growth, insect activity and herbivore consumption (Barrio et al., 2017; Moles et al., 2014). We also considered the mean temperature of the warmest quarter and total precipitation of the warmest quarter as this is widely regarded as the peak season for plant growth and herbivore consumption (Barichivich et al., 2012; Hillebrand et al., 2009).

2. The 3 second STRM Derived Digital Elevation Model (DEM) v1.0 (Gallant et al., 2009) for elevation.

3. The Australian Bureau of Meteorology's gridded dataset for mean annual relative humidity at 3pm at 0.1 degree resolution (available from http://www.bom.gov.au/web01/ncc/www/climatology/relative-humidity/rh15/rh15an.zip) for relative humidity. We used relative humidity at 3pm instead of 9am, as humidity is higher in the mornings in most locations which is not representative of the humidity experienced by plants/herbivores for most of the day (US Department of Commerce).

All values associated with our site locations were extracted from the datasets using the nearest-neighbour interpolation in QGIS v3.24 (QGIS Development Team, 2022).

Data analysis

All statistical analyses were performed in R version 4.2.0 (R Core Team, 2021).

To understand the direction and magnitude of enemy release, we ran Generalised Linear Mixed Models using Template Model Builder (Brooks et al., 2017). We used the amount of herbivory plants received as our response variable, range (introduced or native) as our predictor variable, and included random effects terms for site, species, and individual. As our data contained many zeros, we used the Tweedie family with log-link function to fit our model. The coefficient for range represents the ratio of herbivory in the native to herbivory in the introduced range, on a log scale (i.e., it represents enemy release). Our data did not require any prior transformation as they satisfied all model assumptions.

Next, we tested whether enemy release is affected by the amount of time plants have had to establish in their introduced range we using linear models with the *lm* function in base R (R Core Team, 2021). Our response variable was enemy release (using model coefficients for each species from our first herbivory model) and our predictor variable was time since introduction. We used the species' coefficients from our first model as they accounted for variance in herbivory between individual plants and sites. We used a similar model to quantify the relationship between enemy release and plants' range size in Australia. Enemy release, using previous model coefficients again, was our response variable and log_{10}-range size was our predictor variable.

After analysing the last two models we decided to test whether time since introduction influenced the amount of area that species would end up occupying in their introduced range.

To do this we ran a linear model with our predictor variable as species' time since introduction and response variable as introduced range size using the *lm* function in base R (R Core Team 2017).

Finally, we asked whether climatic conditions and elevation of sites in the introduced range affect the magnitude of enemy release plants experience. Because climate and elevation vary across sites within the introduced range, we calculated introduced-site specific enemy release metrics for each species. We did this by calculating a weighted average of herbivory in the introduced and native ranges (per species per site; details in Appendix S4). Introduced-site specific enemy release for each species was therefore calculated as ln(mean herbivory across the whole native range/mean herbivory for each site in the introduced range). We performed generalised linear mixed models using these site-level enemy release metrics as our response variable, climate traits/elevation of the introduced sites as our explanatory variable, and site and species as random effects terms.

Results

After conducting fieldwork across twelve sites, six countries and two continents, we had recorded 11600 separate visual estimations of herbivory (6142 in the native range and 5458 in the introduced range) for 16 plant species. Consistent with the enemy release hypothesis, we found that overall, our species experience greater herbivory in their native range than in their introduced range (Fig. 2; $P < 0.0001$) with an effect size of 1.88 (95% confidence interval from 1.10 to 2.66). In biological terms, this means that plants in their native range are suffering from 6.55 times more leaf damage than conspecifics in their introduced range. Individually, all 16 species tended towards greater herbivory in the native range, with half being statistically significant (95% confidence intervals did not overlap zero).

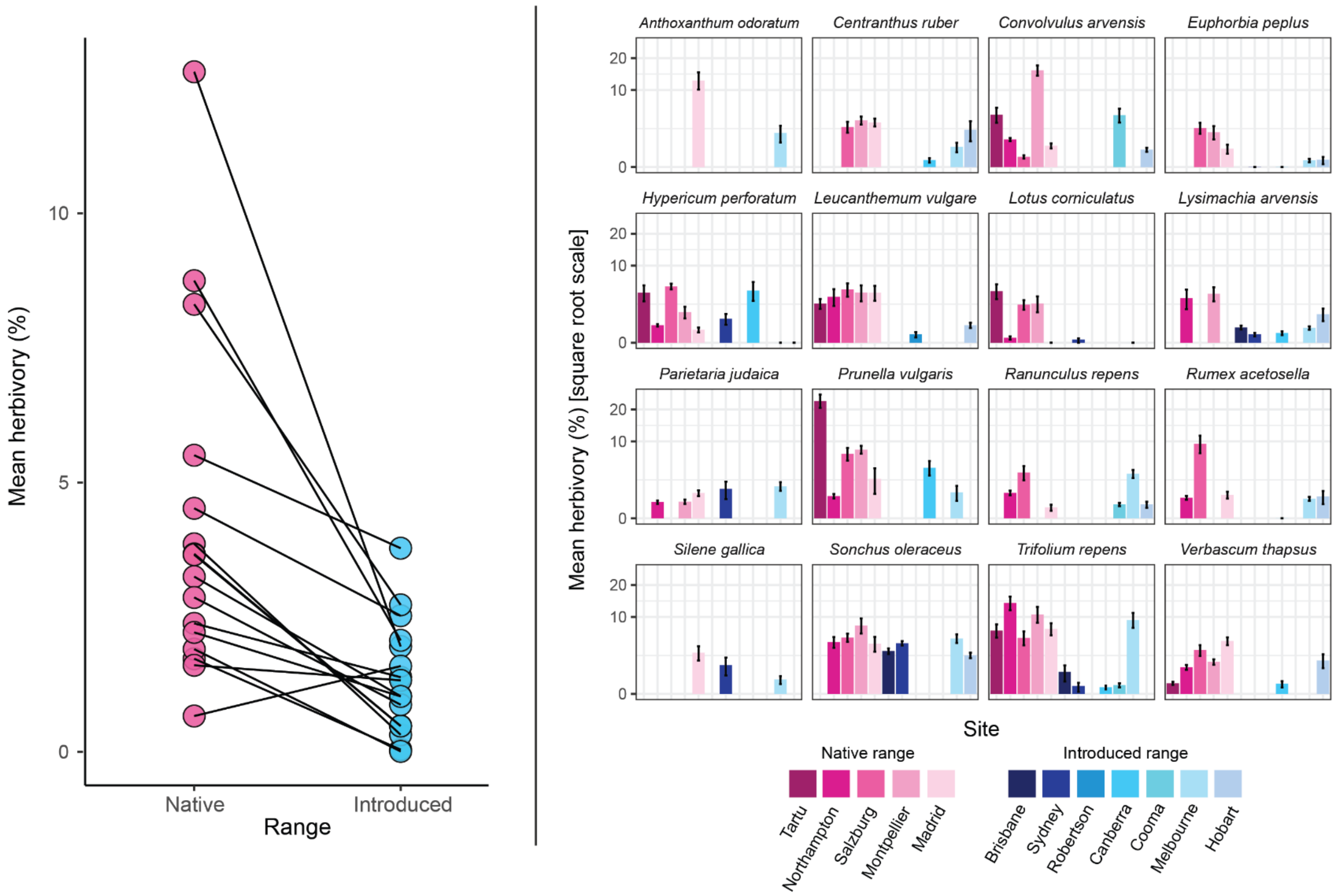

Figure 2. [Left] Comparison of mean herbivory between native (pink) and introduced (blue) ranges for each species site-weighted average herbivory in native and introduced ranges. [Right] Variation in mean herbivory across sites in the native and introduced ranges for each target species. Bars represent means +/- standard error.

Contrary to our prediction, we found no evidence for a correlation between species' degree of enemy release and time since introduction (Fig. 3a; P = 0.14, adjusted $R^2 = 0.09$, $df = 14$, $F = 2.51$).

There was no significant relationship between species' degree of enemy release and the amount of introduced area they currently occupy (Fig. 3b; P = 0.67, adjusted $R^2 = -0.06$, $df = 14$, $F = 0.19$).

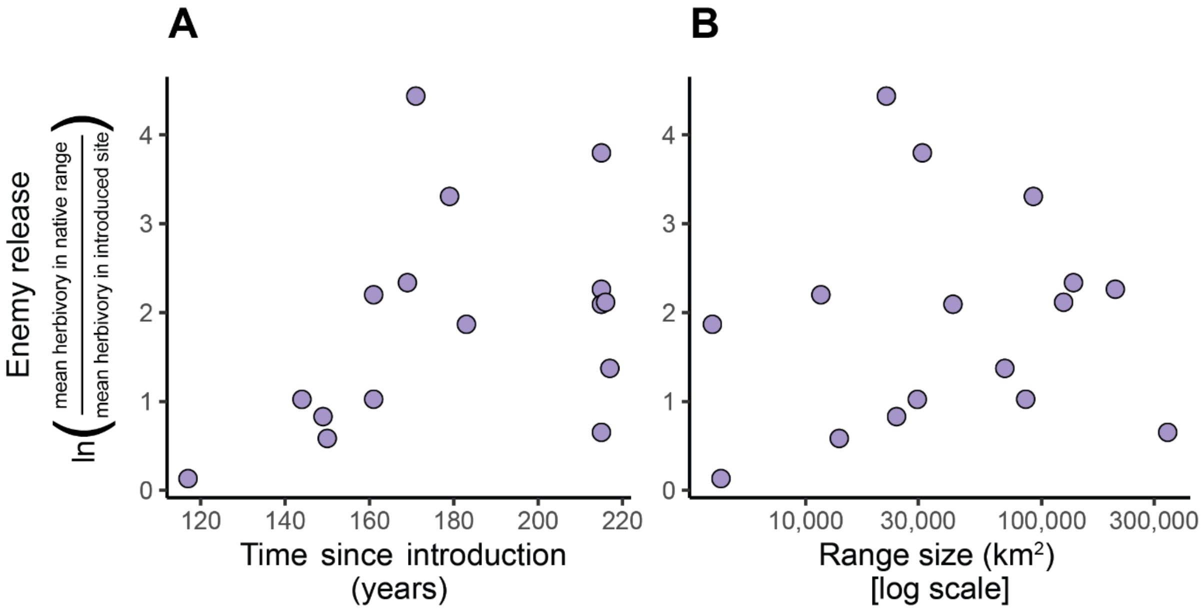

Figure 3. The relationship between plants' (a) time since introduction (P = 0.14) and (b) range size (P = 0.67) in Australia, to their degree of enemy release. Range size is calculated as the sum of grid squares (at 0.05 decimal degree resolution) that are occupied by a species. Each point represents a target species (n = 16). Neither model showed evidence for an association between variables.

Although it was not one of our initial hypotheses, we did notice a positive relationship between species' range size and time since introduction (Fig. 4; P = 0.01, adjusted R^2 = 0.32, *df* = 14, *F* = 7.91).

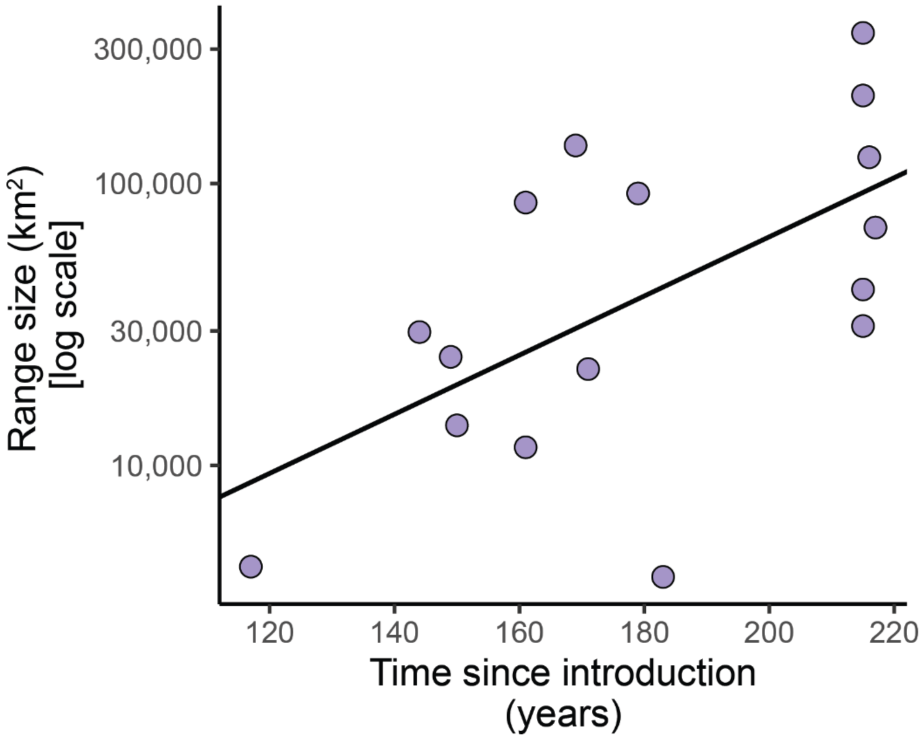

Figure 4. The relationship between species' time since introduction and the amount of introduced area they occupy (P = 0.01, adjusted R^2 = 0.32, *df* = 14, *F* = 7.91). Each point represents one species.

Counter to our predictions, we found no evidence for an association between the magnitude of enemy release and mean annual temperature (Fig. 5a; $P = 0.64$, $n = 46$) or mean summer temperature (Fig. 5d; $P = 0.68$, $n = 46$). We also found no evidence for a relationship between enemy release and annual precipitation (Fig. 5b; $P = 0.87$, $n = 46$) or precipitation of the warmest quarter (Fig. 5e; $P = 0.46$, $n = 46$). Finally, we found no evidence for an association between the amount of enemy release plants receive and elevation (Fig. 5c; $P = 0.5$, $n = 46$) or relative humidity (Fig. 5f; $P = 0.6$, $n = 46$) of their introduced site. That is, none of our climate variables helped to predict when introduced species experience enemy release.

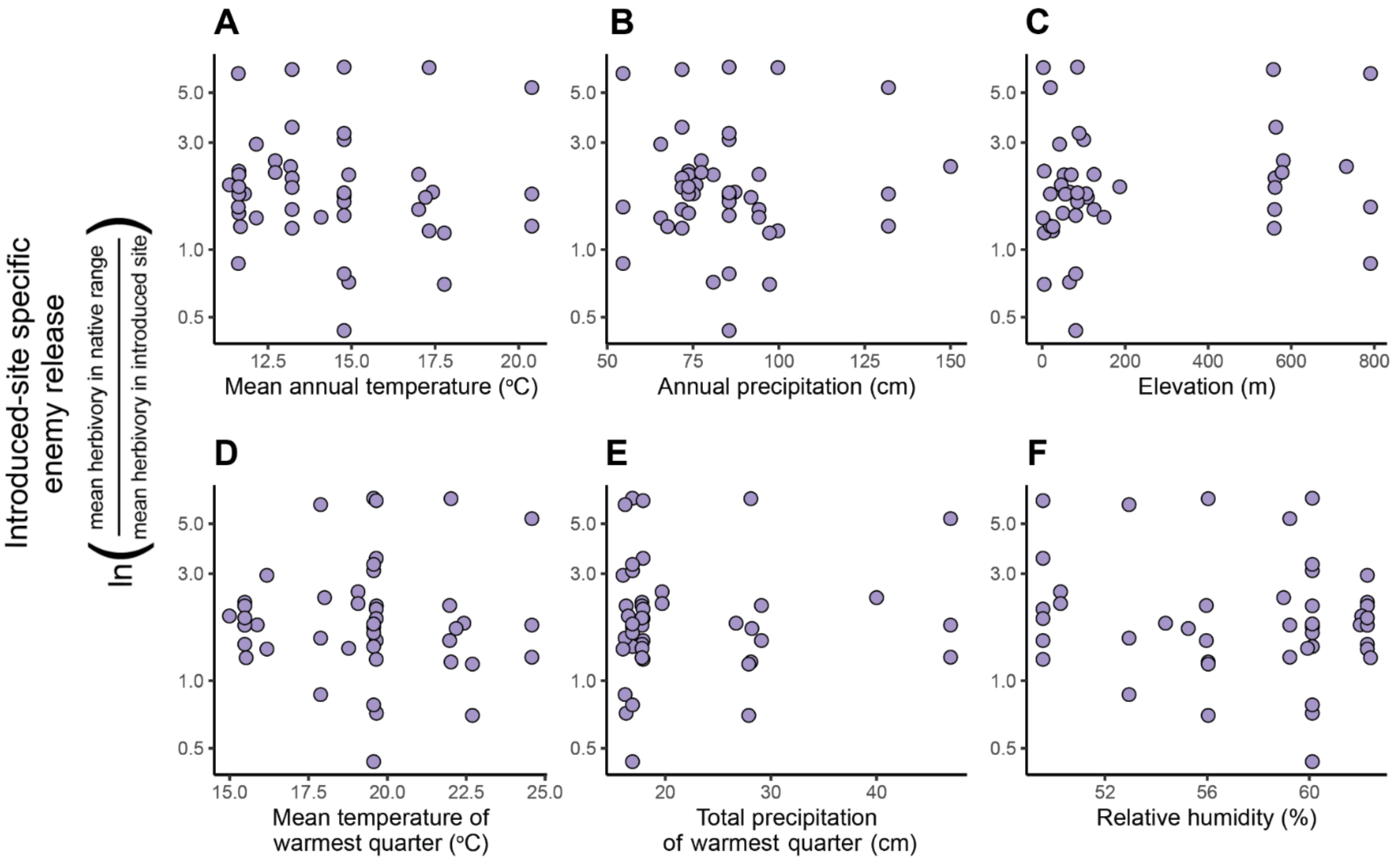

Figure 5. Introduced-site specific enemy release against (a) mean annual temperature (P = 0.64), (b) annual precipitation (P = 0.87), (c) elevation (P = 0.5), (d) mean temperature of the warmest quarter (P = 0.68), (e) precipitation of the warmest quarter (P = 0.46), and (f) relative humidity (P = 0.6). Points represent target species at each site in their introduced range (n = 46). No models showed evidence for an association between variables.

Discussion

We did not find that time, space, or climate are related to the magnitude of enemy release plants experience in their introduced range (Fig 3, 5). This null result is important, as it suggests that enemy release, one of the major factors underpinning the success of introduced species cannot be predicted by the abiotic factors of plants' novel environments. Our study did not encompass the full suite of the world's ecosystems but did include sites ranging in mean annual temperature from 11.3°C to 20.4°C, in total annual precipitation from 54.6cm to 150cm, and in elevation from 2m to 791m. Our findings might help to explain why almost all habitats on earth have been invaded by introduced plants (Barney et al., 2015; Jeschke et al., 2012; Mack et al., 2000). On another note, our findings also suggest that biocontrol, the flip-side of enemy release, should be equally likely to succeed or fail independent from the ecosystems they inhabit.

Knowing the ecological context behind a species invasion is a crucial step to implementing practices to hinder the spread of introduced species (Catford et al., 2022). In most cases, classic biological control is employed to target problematic invasive species with the aim to slow or decrease their population growth with minimal impact on surrounding native species (Clewley et al., 2012). These reductions in invasive populations can be achieved by releasing known above or below-ground herbivores, predators, or pathogens, that are native to the same areas as the invasive species, as controlling agents (Schulz et al., 2019). There are many successful examples of biocontrol around the world (see López-Núñez et al., 2021; Pedler et al., 2016; Portela et al., 2020) and meta-analyses by Stiling & Cornelissen (2005) found that biocontrols can reduce the biomass and reproductive output of weeds by over 80 percent. But not all instances of biocontrol succeed. Failed attempts at biologically controlling invasive plants have been recorded globally (Schulz et al., 2019; Stiling, 1993). Plant species that have been identified as being released from their enemies should theoretically have the highest chance of successful management with biological control, as enemy release likely contributes to their successful invasion (Blumenthal, 2005). However, our study implies that biocontrol is equally likely to be effective under a range of abiotic conditions, and regardless of introduced species' time since introduction into a novel range or range size.

There is much more variation in plants' potential to encounter enemies in the introduced range than originally expected, which might help to explain the lack of correlation between enemy release and time since introduction and introduced range size. For example, a plant that has recently established in a highly disturbed area with a high diversity of other introduced species, may be more likely to encounter compatible herbivores than plants that have established earlier in a more stable, mono-typic habitat. Similarly, a non-native species occupying a smaller area of space, with more generalist herbivores, may experience greater herbivore pressure than plants occupying a more expansive patch of land that houses fewer generalist herbivores.

We did find a relationship between introduced species' geographic spread and the amount of time they have had to establish themselves in their new range (Fig. 5). This finding corroborates many preceding studies in invasion ecology that have also shown that distribution in the non-native range is strongly correlated with time since introduction and demonstrates that our sampling effort is rigorous enough to detect this pattern (Forcella & Wood, 1984; Gassó et al., 2010; Pyšek et al., 2015; Pyšek & Jarošík, 2005; Vila-Gispert et al., 2005; Williamson et al., 2009; Wilson et al., 2007). Remarkably, some introduced plants have been found to colonise local areas at rates of up to 370 metres per year and long-distances at up to 167 kilometres per year (Pyšek & Hulme, 2005).

The lack of a significant relationship between enemy release and abiotic factors such as climate and elevation could arise from herbivory not being explained by these variables (see Appendix S5). Some studies have shown no significant relationship between herbivory and temperature or precipitation (Leckey et al., 2014; Sinclair & Hughes, 2008), while others have found that herbivory increases (Barrio et al., 2017; Kozlov, 2008; Meineke et al., 2019; P. Zhang et al., 2020), or decreases with temperature or precipitation (Adams & Zhang, 2009; Lowman, 1984; Mazía et al., 2012), and others have found mixed results (Lemoine et al., 2014; Moreira et al., 2015). However, even where significant positive correlations have been detected, they tend to have R^2 values below 0.3 (Moles et al., 2014; S. Zhang et al., 2016). Empirical evidence for an effect of humidity and elevation on herbivory is much scarcer, and available research does not explore these relationships at global scales, or across multiple species (Moreira et al., 2018; Reynoso & Linera, 2007).

We collected data from a broad range of species from varying locations in their native and introduced ranges. Our finding that enemy release is not directly related to time since introduction, range size, or climate, is new and valuable information that may influence the trajectory of our use of biocontrols. We hope this study will trigger future research to explore more factors, such as herbivore specialisation or defensive traits, that may affect species success in new ranges, so we may find clearer answers relating to the spread of introduced plants. If we are to conserve and protect Earth's natural ecosystems, of which almost all have been considered invaded by non-native species, then enhancing our understanding of the mechanisms affecting these invasions are critical (Barney et al., 2015).

Author Contributions

ZAX led the project, including administration, data collection, data analysis, interpretation of results, figure preparation, and initial manuscript preparation. JO, RT, BP, VL, RRJ, MP, SR, AU, and MJH provided logistical support, laboratory resources, and contributed to data collection. ES contributed to data analysis, interpretation of results, and visualisation. GMC assisted with spatial data extraction and data analyses. ZAX, SPB, SR, and ATM acquired funds for the project. ATM conceptualised the project and its design (along with SPB), and contributed to supervision, data analysis, laboratory resources, and initial manuscript preparations. All authors contributed substantially to manuscript revisions.

Conflict of Interest

We have no conflict of interest to declare.

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