Characteristics of Australia's alien flora vary with invasion stage

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Abstract

Aim: Directly or indirectly, humans select the plants that they transport and introduce outside of species native ranges. Plants that have become invasive may therefore reflect which species had the chance to invade, rather than which species would become invasive given the chance. We examine characteristics of failed introductions, along with invasion successes, by investigating (a) variation in plant characteristics across invasion stages, and (b) how observed characteristics predict the likelihood of species moving through invasion stages.

Location: Australia.

Time period: 1770s to present.

Major taxa studied: 34,650 plant species, across 424 families.

Methods: We used a comprehensive list of 34,650 plant species that are known to have been introduced to Australia, 4,081 of which are classified as naturalized and 428 as invasive. We represent plant characteristics with categorical growth forms, three functional traits (plant height, seed mass, and specific leaf area) and three factors related to species introduction histories (native regions, purpose, and minimum residence times).

Results: (a) The types of species introduced determine the types of species that naturalize and become invasive; (b) species introduction histories predict the likelihood of species moving through invasion stages; and (c) the numbers of species naturalizing (-15%) and becoming invasive (-15%) slightly exceeds expectation from the "tens rule", which expects that 10% of introduced species naturalize and 10% become invasive.

Main conclusions: Our findings are significant for global biosecurity, indicating that functional traits alone cannot be used to predict a species’ risk of becoming invasive. Rather, evidence suggests that characteristics of species introductions—specifically, a longer time-lag since first introduction and more pathways of introduction—define the relative risks of species moving through invasion stages. This is important for assessing future invasion risks, as future introductions may differ from those of the past. Our work highlights the need to reduce the number of species introduced.
1  |  INTRODUCTION

Human-mediated introduction of species beyond their native biogeographic ranges forms the initial stage of alien species invasion. Once introduced, alien species have the potential to become naturalized, and once naturalized, to become invasive (Blackburn et al., 2011). Alien species are naturalized when they successfully sustain a population in the wild. Naturalized alien species that become dominant in their non-native range, over a broad region and causing negative ecological impacts, are defined as invasive (Blackburn et al., 2011). Invasive species are a major threat to biodiversity and ecosystem function (e.g., Randall, 2007), and can negatively impact social, cultural and economic values (Pyšek et al., 2020), so predicting species that are likely to become invasive is a central aim of biosecurity and environmental policy and management. One of the factors considered in invasive species risk assessments is how the profiles of species that have become invasive in the past compare with profiles of recently, or soon-to-be, introduced species (Pheloung, 1995). However, alien species can only become invasive if they have first been introduced and thus have the opportunity to become invasive (Figure 1). As international trade and travel increase, many more species are being introduced (Seebens et al., 2017), such that the characteristics of current and future introductions may differ markedly from historical introductions (e.g., Dyer et al., 2017). To identify future biological invasion risks, it is thus essential to account for the introduction bias of past invasions. To achieve this, one must look at all introduced species—including those that fail to establish—when examining characteristics associated with species invasiveness (Cassey et al., 2004; Diez et al., 2009; Jeschke & Strayer, 2006; Phillips et al., 2010; van Kleunen et al., 2020; Zenni & Nuñez, 2013).

Previous research and biosecurity measures that aim to understand and manage drivers of biological invasion have largely focused on either (a) ecological processes that affect a species’ movement through invasion stages, or (b) probabilities and sampling effects that are based on the likelihood of a certain number of species becoming naturalized and invasive given the numbers introduced and naturalized (Lockwood et al., 2009). The former involves the assessment of species traits, such as functional traits, as drivers of invasiveness, while the latter relates more closely to the characteristics and consequences of introduction histories. However, species traits can also be driven by introduction histories. For instance, the introduced species pool, and its collection of species traits or characteristics, is a function of human transport and introduction, resulting in biases in the pool of potential invaders (Blackburn & Duncan, 2001; van Kleunen et al., 2020). If most introductions have been for agriculture, for example, then traits of naturalized and invasive species will necessarily reflect that introduction pathway (Kinlock et al., 2022), and risks posed by species introduced for, say, medicine may go unnoticed. Unless introduction bias is accounted for, traits of past invaders may identify which species have had the chance to invade, rather than which species would become invasive if given the chance (Figure 1; Duncan et al., 2019; Maurel et al., 2016; van Kleunen et al., 2010).

A theory related to probabilities of invasion and sampling effects is the tens rule, which posits that 10% of introduced and 10% of naturalized species per family go on to become naturalized or invasive, respectively (Williamson, 1996). However, studies vary in the extent to which they find support for the tens rule (e.g., Jarić & Cvijanovic, 2012; Strayer et al., 2012). For instance, in meta-analyses and empirical research, alien plant naturalization rates have ranged from 9 to 49% for species naturalizing, and up to 60% for naturalized species becoming invasive (Jeschke & Pyšek, 2018). One possible reason for inconsistent support for the tens rule is use of the ratio of naturalized to introduced species to test it. This approach assumes that all introduced species have had enough time to naturalize and become invasive (Caley et al., 2008), which is not a fair assumption. This highlights the importance of including minimum residence times or time-lags in studies of biological invasions (Kowarik, 1995; Rouget et al., 2016).
Here, we use data on 34,650 introduced, 4,081 naturalized and 428 invasive alien vascular plants in Australia to examine the influence of species introduction on the stage of invasion of all alien species known to have been introduced into Australia. Specifically, we address the following questions:

1. How do characteristics of the alien flora vary across invasion stages?

2. To what extent do the species characteristics and introduction histories act as predictors for the likelihood of species moving through invasion stages?

To answer these questions, we analyse data for categorical growth forms, and three functional traits [plant height, seed mass and specific leaf area (SLA)] and three factors related to species introduction histories (native regions, introduction pathway or purpose, and minimum residence times). We expect that species that were introduced earlier have had more opportunity to become invasive than recently introduced species. Australia is a suitable case study for these questions because of its documented history of plant introductions (e.g., Randall, 2007) and its high level of plant invasion (Pyšek et al., 2017; Seebens et al., 2017; van Kleunen et al., 2015) and strong commitment to biosecurity (Murray & Phillips, 2012). Understanding any variations in characteristics across invasion stages can help in identifying drivers for species at risk of becoming invasive in future, and assess the reliability of using functional traits to profile species in biosecurity measures.

2 | METHODS

2.1 | Data compilation

A relational database was compiled within the R software (version 4.1.1) environment for statistical computing and graphics (R Core Team, 2021).

2.2 | Introduced species and taxonomic standardization

The primary list of all known plants introduced to Australia is based on a comprehensive compilation from a variety of historical records and resources, initially comprising 41,158 plants identified to at least species level (Randall, unpublished data). The list of all plant taxa used in this study will be referred to as the “species list” hereafter. Species names were standardized using the Leipzig Catalogue of Vascular Plants (LCVP) version 1.0.4 (Freiberg et al., 2020). LCVP forms the most up-to-date and largest taxonomic reference list for all known vascular plants, including natural (i.e., non-cultivar), hybrid and infraspecific taxa. LCVP incorporates and updates taxonomic information provided by The Plant List (TPL) (http://www.thelist.org/) and TPL’s successor Plants of the World Online (https://powo.science.kew.org/). Taxonomic name resolution was performed using functions in the R package lcvpplants (Freiberg et al., 2020). Names without (a) an “accepted” species name, or (b) a synonym matched with an accepted name, were rechecked using the LCVP fuzzy matching algorithm to resolve orthographic errors (n = 488). Fuzzy matching was set with a maximum distance of one character to reduce the chance of names being matched to the wrong species. Remaining names (n = 1,258) not resolved within LCVP were checked manually using online resources, for example, the Global Biodiversity Information Facility (GBIF; https://www.gbif.org) and Web of Science (https://www.webofscience.com/wos/). Cultivars and names with hybrid formulas (e.g., *Achillea millefolium × Achillea taygetea*) were checked against the Australian Plant Census in the Australasian Virtual Herbarium (https://avh.chah.org.au/). Original names not identified in any taxonomic standardization methods (n = 3) were retained in the species list and noted as “unknown”.

The resulting taxonomically standardized species list contains 34,650 species (84% of the full list of 41,158 taxa), comprising 33,430 accepted species names and 1,220 species names without accepted statuses. The 6,508 taxa that were omitted from the species list were removed because of: (a) duplicate species names [e.g., synonyms (n = 4,323) and/or homotypic synonyms (n = 2,114) listed for the same species]; (b) incomplete or not at species-level names (n = 42), and non-vascular plant species (n = 29). To identify species listed as a synonym in linked datasets, an additional “alternative species name” list was created with all identified synonyms and homotypic synonyms in LCVP and GBIF. GBIF includes synonyms not listed in LCVP, which only incorporates phylogenetic studies making taxonomic decisions on molecular data. This means that synonyms not listed in LCVP might have less taxonomic accuracy, but an increased chance of matching the species with combined datasets, particularly non-standardized historic resources. Alternative names were identified for 10,373 taxa in the species list totalling 26,120 alternative names. Linked datasets described in the following sections were incorporated by initially searching for species names with the accepted species list, followed by searching with alternative names.

2.2.1 | Invasion stage in Australia

Alien species were classified as introduced, naturalized or invasive using global and national checklists (detailed below). The classifications of species in the list are not mutually exclusive, unless otherwise stated. Therefore, all species are classified as introduced, regardless of if they went on to become naturalized or invasive, and the naturalized species pool includes invasive species.

The introduced species list includes all 34,650 species, belonging to 5,006 genera and 424 families. All introduced species are alien plants known to have been introduced (deliberately or accidentally) to Australia at any point in time between 1770 and 2021. The species list contains 4,081 naturalized species (including invasive), belonging to 1,641 genera and 254 families, and 428 invasive species, belonging to 245 genera and 84 families. The naturalization statuses
of species were identified via the “Global Naturalized Alien Flora” (GloNAF) database (van Kleunen et al., 2019), the Australian Plant Census and species with naturalized status in Randall (2017) and Randall (2007). Species with a “casual” or “cultivated” status, based on Randall (2017) and Randall (2007), were excluded from the naturalized subset as they are not defined as having self-sustaining populations and are not uniformly defined, respectively. Once naturalized, some alien species go on to become invasive. Here, the definition for invasive species was interpreted as species that have spread widely from their point of introduction (Blackburn et al., 2011), and have a negative impact, based on definitions in invasive species checklists detailed below. Invasive alien species were identified as invasive in Australia via the Global Invasive Species Database (GISD; http://www.iucngisd.org/gisd/), the Global Register of Introduced and Invasive Species (GRIIS; Pagad et al., 2018) and invasive plant datasets included in the Atlas of Living Australia (ALA; https://www.ala.org.au/).

2.2.2 | Growth forms

Each species was classified by its growth form using a hierarchical method based on combined datasets. The seven growth form classes used here are: fern, forb, graminoid, shrub, succulent, tree and vine. Growth form categories were based on the International Union for Conservation of Nature (IUCN) Plant Growth Forms Classification Scheme (version 1.1) (https://www.iucnredlist.org/resources/classification-schemes). Where relevant, sub-categories (e.g., small, or large trees) were combined to increase sample sizes. In some cases, growth forms are known for certain plant families (e.g., Poaceae). For remaining species, growth form names were standardized, and data sources were weighted based on their methodologies to assign a single growth form for species with more than one growth form. Growth form data were primarily gathered from the GlobalTreeSearch online database (https://tools.bgci.org/global_tree_search.php), TRY Plant Trait Database (version 5; Kattge et al., 2020), and growth form data in Engemann et al. (2016) and Taseski et al. (2019).

2.3 | Functional traits

Data for each species were gathered for three functional traits: plant height, seed mass and specific leaf area (SLA). These traits were selected as they can capture a large part of the ecologically significant differences among species (Díaz et al., 2016; van Kleunen et al., 2010; Westoby, 1998), and they relate to potentially important ecological factors such as range size and competition (Gallagher et al., 2015; Guo et al., 2018; van der Sande et al., 2020), along with anthropogenic factors such as ease of transport (e.g., Von der Lippe & Kowarik, 2012). Additionally, the selected traits are relatively easily measured and more widely available in species trait databases compared to other trait measurements (Kattge et al., 2020). SLA is a physiological and allocation trait representing resource acquisition (e.g., light interception), plant height relates to plant size and can represent competitive performance of a plant species, while seed mass is a fitness trait relating to quality and quantity of offspring (Díaz et al., 2016; Divišek et al., 2018; Westoby, 1998).

Trait data were primarily gathered from the TRY Plant Trait Database (version 5; Kattge et al., 2020) and supplemented with data from AusTraits (Falster et al., 2021), the TraitNET (http://traitnet.ecoinformatics.org), Dryad (https://datadryad.org) and PANGAEA (https://pangaea.de) data portals and publishers. As phylogenetically related species have similar trait values (Divišek et al., 2018; Liao et al., 2020), trait records greater than 4 standard deviations from the arithmetic mean of species, genus or family were excluded from the dataset to exclude potentially erroneous entries, or traits measured at different life stages, following Diaz et al. (2016). Descriptive statistics for numbers of functional traits across growth forms are provided in Supporting Information Table S1.

2.3.1 | Native regions

Global native ranges for alien species were obtained from the GloNAF database (van Kleunen et al., 2019), and supplemented with data from GBIF and the Inventory of alien invasive species in Europe (DAISIE) (Roy et al., 2020). The global map used here contains 285 countries, dependant territories, sovereign states and special areas of geographic interest listed in the ISO 3166 standard, containing the published list of codes and names from 2021. Region delineations were based on the Global Administrative Areas Database (GADM; version 4.04; https://gadm.org/data/data), with all GADM areas aggregated by names in the International Organization for Standardization (ISO) 3166 list. For each region in the final map (e.g., countries and islands) a count of species was added where an alien species in Australia was listed as being from that country, island, or an area (e.g., continent) that overlaps with the region in our map. This means that if, for example, a species was listed as being native to Europe, it was counted as one in each individual European country. The region resolution (e.g., country or continent) for each native species entry is provided within the database based on the Biodiversity Information Standards (TDWG) (levels 1–4) for geographic regions.

2.4 | Introduction pathways

Pathways are the human-mediated means by which plants are introduced (deliberately or not) to regions beyond their native range (Randall, 2017). Introduction pathways were compiled from Randall (unpublished data) and supplemented with literature and datasets where pathway information could be extracted (e.g., lists of cultivated plants for agricultural purposes). Species were assigned to six key pathways for plants (contaminant, crop, forestry, medicinal, ornamental and pasture) as originally defined in Randall (unpublished data). Contaminant species were identified as those unintentionally introduced, for example, with a commodity (Pyšek et al., 2011). The
remaining pathways were intentional introductions and their definitions are as follows: crops and pasture are plants promoted as food for humans and for ground cover, and plants used for livestock grazing, respectively (Randall, 2016); forestry species are trees used for commercial and environmental reasons (Cook & Dias, 2006; van Kleunen et al., 2020; Virtue et al., 2004); the medicinal pathway includes plants traded among herbal medicine enthusiasts and sold in nurseries primarily for use in herbal medicine; the ornamental pathway was assigned where a species was present in an ornamental plant commodity resource such as nursery catalogues. Where a species had more than one pathway, all relevant pathways are listed for that species along with a count of unique pathways.

2.4.1 Minimum residence times

Minimum residence times (MRTs) were calculated to account for differences in the length of time since species were introduced to Australia (Kowarik, 1995). First records were obtained from: the Atlas of Living Australia (https://www.ala.org.au/), the first recorded occurrence in Australia in GBIF, dates from digitized museum collections including the Colonial Plants Database (http://sydneylivingmuseums.com.au/research-collections/catalogues-research-tools/colonial-plants-database), herbaria records from the Australasian Virtual Herbarium (https://avh.chah.org.au/) and the Alien Species First Records database (Seebens et al., 2017). The Australian Virtual Herbarium records include earliest records for when introduced plants were first noticed in the “wild” (i.e., already naturalized), as well as first records that include samples from gardens, crops, pastures, etc. MRTs based on first records in the wild or gardens, etc. are noted as being less reliable as they will have been first introduced sometime earlier. To estimate MRT, the year of the earliest record was subtracted from the year 2021.

2.5 Statistical analyses

Statistical analyses were conducted using R (version 4.1.1; R Core Team, 2021). Unless otherwise stated, figures were produced using the package ggplot2 (Wickham, 2016).

2.5.1 Functional traits across invasion stages

Non-metric multidimensional scaling (NMDS) ordination plots were produced using the R package vegan (Oksanen et al., 2013) to visualize introduced, naturalized and invasive species pools in trait space, based on the three functional traits used here. The Bray–Curtis similarity index and analysis of similarity (ANOSIM) were used to detect significant differences in trait space occupied by species across invasion stages. Species traits were assessed across invasion stages for all species, and for species divided into growth form categories where sufficient data existed. The growth form plots are used to account for expected variations in trait ranges across growth forms (e.g., taller trees). Additional NMDS analyses were carried out using an alternative dataset to account for missing functional trait values (Supporting Information Figure S2); methods are based on those in Divíšek et al. (2018). First, missing values were added based on the mean of species of the same genera within the list of alien species in Australia. Where values for the genera were missing, the mean of the species in the same family within the list of alien species in Australia were added. Remaining missing values were added based on the mean of species of the same genera, followed by family where genus-level data were not available using functional trait data from the TRY Plant Trait Database (version 5; Kattge et al., 2020) and AusTraits (Falster et al., 2021). ANOVA was used to compare trait means where distributions were normally distributed. Where data were not normal, nonparametric Kruskal–Wallis tests were performed (Supporting Information Figure S1).

2.5.2 Introduction histories across invasion stages

We assessed whether the numbers of naturalized and invasive species for each plant family were over- or under-represented, based on observed numbers of introduced species. A randomization approach was used, based on methods in Blackburn et al. (2010) and Su et al. (2014). The difference between observed and expected numbers of naturalized and invasive species within each family is based on a random selection of numbers of species introduced to Australia in each family. Ten thousand random simulations of numbers naturalized from the pool of introduced species were computed to generate a frequency distribution of the number of species in each family. The observed number of naturalized species within each family is considered to be an over- or under-representation if it exceeds the maximum or minimum number derived from simulations of numbers naturalized from the pool of introduced species, and likewise for invasive species from the pool of naturalized species. In addition, relative proportions of known species from each family globally are provided in Supporting Information Figure S3. A map of native region distributions for alien species across invasion stages was created using the rworldmap R package (South, 2011). The ggalluvial R package (Brunson, 2020) was used to visualize introduction pathways. Nonparametric Kruskal–Wallis tests were performed to compare MRTs across invasion stages. MRT was additionally compared for different growth forms to account for differences in generational stages (e.g., trees often have longer generation times than other growth forms).

2.5.3 Predictors for the likelihood of species moving through invasion stages

Multivariate adaptive regression splines (MARS) were used to identify predictors of species status in Australia, using trait values (SLA, height, and seed mass), number of introduction pathways, number of
species introduced per family, and minimum residence times. MARS was selected as it is a nonparametric approach that can model continuous and categorical data and can identify nonlinear and multidimensional relationships. The root-mean-squared error (RMSE) was used to select the optimal model, using the smallest value. MARS provides a hierarchy for the importance of covariates as predictors of species status. The ranking of variables is based on the goodness-of-fit of models and is measured by the generalized cross-validation (GCV) value. The earth R package (Milborrow, 2021) was used to determine predictor variables and interactions between modelled variables.

3 | RESULTS

3.1 | Introduction histories across invasion stages

The naturalized species pool includes 254 plant families, 7 of which were over-represented and 4 were under-represented based on 10,000 random simulations of numbers of naturalized species per family from the pool of introduced species. The invasive species pool includes 84 plant families, 2 of which were over-represented and 2 were under-represented from the pool of naturalized species (Figure 3 and Supporting Information Table S3). Numbers of naturalized and invasive species per family were greater for families with more species introduced. These increases were best fit to nonlinear models, and slightly exceeded the tens rule (Williamson, 1996) with around 15% of introduced and naturalized species going on to naturalize or become invasive, respectively. In general, more species were introduced to Australia from families that had more species globally (e.g., Asteraceae; Supporting Information Figure S3).

Patterns in native (source) regions for alien species in Australia were similar across invasion stages. The United States, United Kingdom and Argentina were consistently the biggest donors of alien species (Figure 4). The ornamental pathway was the most common reason for species introductions, followed by medicinal and crop, and to a lesser extent contaminant, pasture and forestry (Figure 5). Of all introduced species with pathway data ($n = 30,721$), 35% were introduced for multiple purposes, including accidental contaminants in some cases. Most invasive species (78%) and most naturalized species (52%) had multiple introduction pathways (Supporting Information Figure S6). Minimum residence times increased significantly across invasion stages, both when all species were pooled together and divided by growth form (Figure 6). Therefore, the earlier a species was introduced the more likely it was to be naturalized or invasive.

3.2 | Functional traits across invasion stages

Introduced, naturalized and invasive species occupied similar overlapping areas in multivariate trait space with no significant differences identified by ANOSIM (global $R = -.03$, $p = .99$). Similarly, ANOSIM did not identify any differences across invasion stages for different growth forms ($p > .05$). Additionally, using a dataset with missing functional trait values imputed, no significant differences were found across invasive stages for all species (ANOSIM global $R = -.03$, $p > .05$) or within growth forms ($p > .05$) (Supporting Information Figure S2). These results suggest that naturalized and invasive species were more or less random subsets of the introduced species pool when it came to these three traits (Figure 2).

Univariate analyses within different growth forms showed that invasive graminoids were generally taller than introduced and naturalized graminoids, and forb height increased across invasion stages, whereas tree height decreased across invasion stages (Figure 2 and Supporting Information Figure S1). Both graminoids and forbs that are naturalized had larger leaf areas compared to those that are introduced or invasive. Introduced trees had larger leaves compared to naturalized and invasive trees. Seed mass was smallest for naturalized graminoid species. For forbs, seed mass increased across invasion stages. The trend was the opposite for trees, with seed mass decreasing across invasion stages (Supporting Information Figure S1 and Table S2).

3.3 | Predictors for the likelihood of species moving through invasion stages

Results from the MARS model indicate that minimum residence times, followed by number of introduction pathways, had the greatest impact on species’ stage of invasion, and to a lesser extent numbers of species introduced per family. Species were more likely to move through invasion stages as MRT, number of introduction pathways and numbers of species introduced per family increased (RMSE for selected model = 0.58; Figure 7 and Supporting Information Figure S8). The likelihood that a species moved through invasion stages was unrelated to height, seed mass or SLA, the three traits examined in this study.

4 | DISCUSSION

Using a dataset of all known alien plant species introduced to Australia, we found that how, and especially when, species were introduced largely determined which species naturalized and became invasive. For the 34,650 alien species introduced to Australia to date, our findings suggest that species’ introduction histories have driven species’ relative invasion success. Minimum residence times (MRTs) followed by number of introduction pathways were the most important predictors of the invasion stage attained by an alien plant. Longer MRTs and greater numbers of introduction pathways per species increased the likelihood of species moving through invasion stages. There were no overarching relationships between invasion stage and the three functional traits we investigated, though there were some differences among growth forms, with height being positively associated with forb invasion stage and negatively associated...
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Together, our results indicate that: (a) introduction is the critical stage of invasion, and (b) the opportunities provided by human selectivity are the key determinants of whether a species becomes naturalized and invasive.

4.1 Introduction histories vary across invasion stages

Drivers of a species’ movement through invasion stages include: the probabilities of a species going on to naturalize or become invasive, based on numbers introduced, and ecological drivers that may affect a species ability to spread in its non-native range. MRTs increased across invasion stages. Species introduced earlier were more likely to have moved through invasion stages to become invasive. This finding means that the numbers of both naturalized and invasive species in Australia will increase over time, even if no new species are introduced. This so-called invasion debt is consistent with previous research showing the importance and prevalence of time-lags in biological invasions (Duncan, 2021; Kowarik, 1995; Rouget et al., 2016).

Pathways associated with introduced species were generally consistent across invasion stages, indicating that more introductions of plants for each pathway led to more naturalized and invasive plants. In agreement with other research (Dehnen-Schmutz et al., 2007; Mayer et al., 2017; van Kleunen et al., 2018, 2020), the ornamental pathway was the main source of species introductions. However, overall, a majority of naturalized and invasive species had multiple introduction pathways. The increase in pathway numbers across invasion stages, further highlight the importance of colonization pressure and propagule pressure, which are known to be important drivers of invasion success (Blackburn et al., 2020; Duncan, 2016; Duncan et al., 2019; Lockwood et al., 2009; Pysek, Novoa et al., 2020).

The introduction of more species from a geographic region leads to more naturalized and invasive species from that region (Figure 4). The regions with the most species across invasion stages are consistent with current and historic trade and migration connections with
Australia (e.g., human migrations from Europe). In some cases, species may not have been directly introduced to Australia from their native region, rather from donor regions (regions where an alien species has been introduced, leading to their introduction from that region). Furthermore, regions could potentially be over-represented if their flora is better known and therefore has greater representation within datasets.

Our study revealed that the number of invasive species from each family is largely a function of the number of species introduced from each family: as more species per family are introduced, more go on to naturalize, and as more naturalize, more go on to become invasive. Based on the trends in Figure 3, the numbers of naturalized and invasive species for 95% of families matched expectations based on numbers of introduced and naturalized species respectively. Our findings slightly exceeded the tens rule, with around 15% of introduced and naturalized species going on to naturalize or become invasive, respectively. This highlights the importance of introductions in driving subsequent invasions. Along with being time dependent, rates of movement through invasion stages can vary spatially, with potential drivers such as colonization pressure and invasion meltdown taking effect (Jeschke & Pyšek, 2018). Therefore, our observed increase in the numbers of species naturalizing and becoming invasive may be down to more species having time to move through invasion stages, potentially compounded with additional drivers at different spatial scales.

Of 343 plant families naturalized and invasive in Australia, 15 were over- or under-represented in our analyses. For those families, species could be interpreted as having characteristics making them more or less successful in moving through invasion stages. In our study, drivers of plant families with over- and under-represented species numbers based on random simulations appear to be related to probabilities and sampling effects, introduction histories and/or ecological processes. For instance, both Poaceae (grasses) and Asteraceae (daisies) were over-represented among naturalized species. These families are within the top five largest floral families in the world (World Checklist of Selected Plant Families: https://powo.science.kew.org/). Explanations for their over-representation include both probabilities and sampling effects, for example, where globally over-represented species are more likely to be introduced (Pyšek et al., 2017), and ecological processes, for example, where their broad biogeographic ranges may lead to species from these families being more successful in naturalization as they tolerate larger climatic gradients (Diez et al., 2009). Furthermore, relating to introduction histories, species in relatively smaller over-represented families, such as Cyperaceae, also have long histories of introduction for agricultural purposes, which has previously been found to lead to over-representation of these families across all invasion stages (van Kleunen et al., 2020).

Orchidaceae and Bromeliaceae were the only invasive families with under-represented numbers. One potential explanation is that
FIGURE 4  Global map of native regions for alien species (a) introduced, (b) naturalized and (c) invasive in Australia. Scales are shown as a proportion of species (introduced, naturalized or invasive) that are native to region. In the legend after proportion scales, Sn provides the minimum and maximum numbers of species in each region for that proportion range. The numbers of species with native region data are: introduced 21,633 of 34,650 (62%), naturalized 4,081 (all naturalized species) and invasive 428 (all invasive species). To aid visualization, circles represent smaller islands. The circles are located based on the centroid of the island region. Region delineations are based on the Global Administrative Areas Database (GADM). Maps were generated in R using the rworldmap R package (South, 2011). The map is projected using the Equal Earth Map projection (Šavrič et al., 2019). Species indicated as native in Australia include those that are native in region(s) of Australia and have been introduced to region(s) where they are not native. A map with logarithmic scales is provided in Supporting Information Figure S5.
Functional traits across invasion stages

Plant functional traits and ecological processes that can affect the ability of a species to move through invasion stages have been identified in previous research (e.g., Catford et al., 2016; Muth & Pigliucci, 2006; Palma et al., 2021; van Kleunen et al., 2010; van der Sande et al., 2020). However, our findings suggest that trends in the three functional traits assessed here reflect the histories of human introductions rather than signalling traits associated with species' inherent ability to become invasive (which we term their invasiveness herein). The overall trend was that, based on the three functional traits used here, the types of species introduced determine the types of species that naturalize and become invasive. This was true for all alien species treated as a single group and split by growth form.

In some instances, our findings agreed with research on invasiveness traits, which can be driven by both introduction histories (e.g., trait selection) and ecological processes (e.g., traits that may help species move through invasion stages). For instance, in a meta-analysis of traits relating to performance, van Kleunen et al. (2010) found that invasive species generally had higher trait values relating to performance (e.g., plant height). However, while our univariate findings for height were higher for invasive graminoids and forbs, the opposite trend was observed for trees and results were inconclusive for remaining growth forms in the analysis (Supporting Information Figure S1). Based on the three traits assessed here, there was some agreement with the dimensions of invasiveness (Palma et al., 2021). For instance, in multivariate trait space, invasive species generally had smaller seed mass and SLA, relating to competitive functions. Other recent studies have found differences in traits among native, naturalized and invasive species (Divišek et al., 2018; Guo et al., 2022). These studies indicate that invasive species can have particular traits that make them more likely to progress through invasion stages. Potential reasons for differences in functional traits across invasion stages relate to methodology, particularly that—in
FIGURE 6 Boxplot comparisons of minimum residence time (MRT) distributions across invasion stages for (a) all data, (b) forbs, (c) graminoids and (d) trees, where differences across invasion stages are statistically significant. The numbers of species with MRT data are: introduced 22,197 of 34,650 (64%), naturalized 4,081 (all naturalized species), and invasive 428 (all invasive species). Data are shown on a logarithmic scale. Different letters indicate nonparametric Mann–Whitney two-tailed significant differences. The thick horizontal line in each box indicates the median. The bottom and top of each box indicate the 25th and 75th percentiles, respectively, and the vertical lines (whiskers) represent the maximum/minimum value. Outliers are indicated by circles outside the range of whiskers. All MRT results for growth forms are included in Supporting Information Figure S7.

FIGURE 7 Ranked multivariate adaptive regression splines (MARS) used to derive the importance of predictors for species status (InvStage) (introduced, naturalized and invasive). (a) Importance is based on impact upon generalized cross-validation (GCV) statistic values as predictors are added to the model. Predictors include minimum residence time (MRT), total number of pathways (pathway count), and total number of species introduced for the family to which each species belongs. The numbers of species with complete data for included predictors are: introduced 22,197 of 34,650 (64% of species), naturalized 4,081 (all naturalized species) and invasive 428 (all invasive species). (b) Partial dependance plot where the coloured scale indicates relatively low (purple) to relatively high (yellow) values for combined variables [e.g., invasion stage or status is higher (where: 1 = introduced, 2 = naturalized and 3 = invasive) with the longest residence times and largest numbers of pathways].
contrast to Guo et al. (2022) and Divíšek et al. (2018)—our study used all introduced species. Therefore, while in our findings, the overall trait space occupied by all introduced species defines the trait space occupied by all naturalized and all invasive species, additional traits not assessed here may have been important across invasion stages.

5 | CONCLUSIONS

Our findings indicate that: (a) the types of species introduced determine the types of species that naturalize and become invasive, (b) species’ introduction histories predict the likelihood of species moving through invasion stages, and (c) based on the functional traits we examined, the types of species introduced determine the type of species that naturalize and become invasive. While we focused on Australia in this study, our findings are notable for biosecurity protocols that rely on functional trait profiles. While introduction histories are sometimes used in biosecurity measures (e.g., Randall, 2016), this paper highlights the importance of gathering and incorporating such information into biosecurity protocols.

The findings of this paper highlight the importance of reducing overall numbers of species that are introduced beyond their native range globally, as the introduction of new species provides opportunities for some of those species to naturalize and become invasive given time. Our work also emphasizes the value of documenting species introduction histories, including the purposes and pathways of introduction. This information can be used in biosecurity assessments and will facilitate increased understanding of biological invasion processes, including introduction.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://figshare.com/projects/Characteristics_of_flora_introduced_to_Australia/160043.
**BIOSKETCHES**

**Angela Bartlett’s** PhD was funded by the London NERC Doctoral Training Partnership (DTP). Her interests cover a range of disciplines, including invasion ecology, aquatic catchment management and global change. She is particularly interested in integrating empirical and theoretical research to improve targeting of interventions for environmental challenges we face in a changing world.

Angela’s research is focused within the macroecology sub-field, where the development of large ecological datasets and databases is used to explore spatial and temporal patterns in the human-mediated movement of species around the world, and how this filters through to biological invasion processes.

**SUPPORTING INFORMATION**

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