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Factors influencing naturalisation success in horticultural species: a case study using planting records from the inception of a planned city

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Abstract Worldwide, many invasive plant species are garden escapees. While weed risk assessment can identify new plant introductions with weedy potential, it does not address the large number of non-native plant species already present in many regions, the majority of which are horticultural species. Here we evaluate the drivers of plant naturalisation success using historical data on the horticultural woody species planted in Canberra, Australia. Canberra provides a unique opportunity to study plant naturalisation as it is a planned city with extensive horticultural plantings originating from government nurseries that kept extensive records documenting the planting efforts from the city's inception. We identified factors linked to naturalisation success in 1439 horticultural, woody, non-native species planted in Canberra over 150 years by fitting univariate and multivariate regression models, and identified both direct and indirect effects using path analysis in a Bayesian framework. We found species were more likely to naturalise with greater planting effort, longer residence time, smaller seeds and dispersal mechanisms linked to wind and animal vectors. Cold-hardy and tall plants were also more likely to naturalise, although cold hardiness and height mostly affected naturalisation success indirectly via planting effort. These findings can aid in generating quantitative risk assessment models to predict woody garden species that would naturalise and pose the greatest risk of becoming invasive in the future.

Keywords Anthropogenic factor · Deliberate plantings · Garden escapees · Naturalisation · Path analysis · Species traits

Introduction

Horticulture is the major pathway by which non-native plant species are introduced to new regions and escape to establish self-sustaining wild populations (naturalise) (Combellack 1989; Reichard and White 2001; Dehnen-Schmutz et al. 2007; van Kleunen et al. 2018). Of the world's approximately 13,000 naturalised plant species, most were introduced for horticulture and derive from an estimated pool of 170,000 plant species cultivated in gardens and parks around the world (Niemiera and Holle 2008; van Kleunen et al. 2018). The increasing rate at which new plant species have been introduced for horticulture over the

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last several centuries, coupled with a time delay (lag) of often decades to centuries between the introduction of a species for cultivation and its escape into the wild (Kowarik et al. 1995; Huff 2003; Crooks 2005; Theoharides and Dukes 2007; Duncan 2021), means there are likely to be many cultivated species that are capable of naturalising but are yet do so, with those species yet to naturalise creating an invasion debt (Essl et al. 2011; Rouget et al. 2016; Haeuser et al. 2018). Consequently, it is imperative to understand the processes that enable some introduced species to escape cultivation and become naturalised. Such understanding would assist managers in identifying introduced species with the potential to naturalise in the future and hence to quantify and manage the risk associated with the current invasion debt (Reichard and White 2001; Caley et al. 2008; Pemberton and Liu 2009).

Because the time-lag between species introduction and naturalisation can be decades to centuries, many studies have relied on historical records of introductions to identify species that have succeeded or failed to naturalise, with a focus on identifying traits that characterise successful invaders (McIntyre et al. 2005; Pysek et al. 2007; Diez et al. 2009; van Kleunen et al. 2010; McKnight et al. 2017; Peoples and Goforth 2017). Several challenges confront these studies. First, historical records can be difficult to gather and are often incomplete, potentially missing species that were introduced but failed to naturalise. Second, among studies that have obtained historical data, some measure of introduction or planting effort is often the strongest predictor of whether plant species have naturalised or not (Rejmánek and Richardson 1996; Dehnen-Schmutz et al. 2007; Pysek et al. 2009; Maurel et al. 2016). Nevertheless, data on historical planting effort is difficult to obtain and often derived from indirect measures such as the frequency at which plants are listed in nursery catalogues (Mulvaney 1991; Caley et al. 2008). Third, the pool of species introduced for horticulture, the timing of introductions, and the frequency at which species are planted in parks and gardens are in large part driven by human preferences. Species with certain desirable traits, such as showy flowers or the ability to tolerate a wide range of growing conditions, may have been introduced by people early on and planted widely (Mack and Lonsdale 2001). Because both residence time and planting effort are strong determinants of naturalisation probability, traits reflecting human preferences may be indirectly linked to naturalisation success through relationships with the timing of introductions and planting effort. Few studies have attempted to untangle these direct and indirect relationships, and to distinguish traits that directly influence naturalisation success from traits indirectly associated with success through human preferences for early introduction and widespread planting (but see Mack and Lonsdale 2001; Gravuer et al. 2008; Maurel et al. 2016; Peoples and Goforth 2017).

The aim of this study is to examine a unique case study where we have extensive historical planting records from the inception of a major city in Australia. This case study provides a unique opportunity to untangle the direct and indirect drivers of plant naturalisation success. We analyse records documenting in detail the planting history and naturalisation of non-native woody species introduced for horticulture in Canberra, Australia. Being the new capital of Australia, the city of Canberra was planned well before it was officially established in 1913. The city was originally located in a predominantly treeless landscape that has since been converted into a 'garden city' resulting from the planting of approximately twelve million trees (Anon 1980; Mulvaney 1991). Most of this planting was undertaken with the assistance of government agencies. These agencies kept extensive records, which have been archived, providing a history of planting activities from the inception of the city, a situation perhaps unique globally. The planting records are remarkably comprehensive, providing an account of the timing of introductions and planting effort associated with individual species. In addition, records of the non-native plant species planted in the area following settlement of the region by Europeans in the 1830s, some 80 years prior to the establishment of Canberra, have also been compiled (see Mulvaney 1991). We use these historical records to identify the non-native woody species planted in Canberra and derive an index of planting effort for each species. We then used herbarium and natural history records to identify the non-native woody species that have naturalised in Canberra, and examined relationships between naturalisation success and plant traits hypothesised to influence naturalisation success (cold hardiness, plant height, seed mass and dispersal mode), and two factors linked to human preference, residence time and planting effort. Our aim was to untangle the direct and indirect drivers of naturalisation success, taking advantage of the detailed data on planting effort that is not available in most studies.

Materials and methods

Study location

In 1909 a region of south-east New South Wales was selected as the location for Australia's new capital city of Canberra. The Canberra region was part of the traditional lands of the Ngunnawal people but had been settled by Europeans in the 1830s and as a result converted to farmland. At the time of European settlement, much of the area surrounding the proposed city was a largely treeless plain. Prior to official establishment of the city in 1913, a government nursery was constructed in 1911 at a site within the future city boundary called Yarralumla (hereafter Yarralumla Nursery) for the purpose of producing large numbers of plants, primarily trees and shrubs, for planting throughout the parks, gardens and streets of the city as it developed, later also providing residents of Canberra with plants to grow on their properties (Shirley 2008; Coltheart 2011). Canberra (Latitude: 35.27°S, Longitude: 149.12°E; (Supplementary information, Fig. SI 1)) is at an elevation of around 570 m above sea level, has a mean maximum and minimum temperature of 20.0 °C and 7.1 °C, respectively, and an average annual rainfall of 636 mm. During winter, the temperature regularly drops below − 2 °C; the average minimum temperatures in June, July, and August in Canberra are 1.4 °C, 0.0 °C, and 1.3 °C respectively (Australian Government-Bureau of Meteorology 2018).

Data collection

We used an existing database of historical planting records for non-native woody species, including shrubs and trees, planted in the Canberra region that was compiled by Mulvaney (1991). This dataset came from four sources: (1) records of plantings prior to the establishment of Canberra, spanning the period 1830 to 1911, taken from historical descriptions of the region and records from nurseries known to have supplied plants to the Canberra area; (2) records from the Yarralumla Nursery, a government-run nursery established for the purpose of growing plants for roadside, park and amenity plantings throughout the city, spanning the period 1912 to 1990; (3) records from a local private commercial nursery 'Willow Park', spanning the period 1932–1990; and, (4) information contained in several editions of the book 'The Canberra Gardner' (Anon 1980) covering the period 1948 to 1982. The dataset thus covers plantings over a 150-year period from the beginnings of European settlement (around 1840) until 1990.

Most records derive from the Yarralumla Nursery, which kept detailed records of the plants that were grown and planted throughout the city. Due to time constraints, as the records had not been digitised, Mulvaney (1991) randomly selected 23 years that spanned the period 1912–1984, searched the archived records for each year, and counted the number of individuals of each woody plant species recorded as having been planted in Canberra during that year. At least two years were sampled in each decade from 1910 to 1980, and we assume the years chosen provide a representative sample of the plantings that occurred throughout this period. The Yarralumla Nursery data were supplemented with data from other nurseries, particularly to cover periods prior to Canberra's establishment. Full details of the methods used to collate the planting data are presented in the Supplementary Material (SI 1).

For each species, the total number of plantings were summed across years to create an index of planting effort or propagule pressure. In addition, the earliest recorded year of planting for each species was recorded. Because records were taken from a subset of years, and hence the exact year of first planting is not known for most species, each species was assigned to one of eight introduction periods: < 1850, 1851–1870, 1871–1890, 1891–1910, 1911–1930, 1931–1950, 1951–1970, 1971–1990.

In collating the database, Mulvaney (1991) resolved a lot of nomenclatural issues and standardised the species names. We further updated the nomenclature by comparing the species names on Mulvaney's list with the names listed in 'The Plant List' (http://www.theplantlist.org, accessed on 10/03/2017), using the R Package *Taxonstand* (Cayuela et al. 2012) in R (R Development Core Team 2016). Using *Taxonstand*, each species on Mulvaney's list was identified as having a name that was currently accepted, was a synonym, was unresolved, or was not in the Plant List and hence assigned a missing value. For species names identified as synonyms, we updated the name to the currently accepted name for that species from The Plant List. For unresolved or missing names, we used additional sources to resolve the nomenclature, including the Atlas of Living Australia (Atlas of Living Australia, 2017, http://www.ala.org.au/) and CABI (CABI 2017, https://www.cabi.org/isc/). The updating of species names resulted in some synonyms with the same accepted name. In such instances, we combined the data for taxa with the same name as follows: (a) where introduction periods differed, we used the earliest introduction period, and (b) we summed the planting effort. For each species, we extracted the plant family name from The Plant List.

Mulvaney's database included plantings of native species, which we removed because our study focused on non-native species only. We identified native species in the database using the list of native plant names in the Australian Plant Name Index (APNI, 2014, https://www.anbg.gov.au/apni/). First, we updated the APNI list using *Taxonstand* as described above, so that both lists shared a common nomenclature. We then removed all species identified as Australian natives from the Canberra planting database, and then identified and removed all herbaceous species except tall species with woody stems, such as bamboos, which we classed as woody. The original database that Mulvaney (1991) collated included 2,517,377 individual planting records for 2147 species. After updating the nomenclature and removing the native and non-woody species, our final dataset comprised 1,618,435 individual planting records for 1439 species.

To create a list of woody species reported as naturalised in the Canberra urban area, we first extracted a list of the non-native species collected in the ACT region from the Australian Virtual Herbarium (AVH: https://avh.chah.org.au/). As this list derives from herbarium collections, it contains only naturalised species verified through herbarium specimens. To ensure that each record represented a naturalised species, we removed any records that contained the words "native" or "cultivated" in the "establishment means" data field. We then narrowed the records down to those collected within urban Canberra on the basis that records of naturalised plants in this area would most likely have originated from local plantings. We defined the Canberra urban area as a rectangle corresponding to the latitude range: 35°09′ 53″ S to 35°33′ 14″ S and longitude: 148° 54′ 20″ E to 149° 26′ 17″ E. This rectangular area included all of urban/suburban Canberra (Supplementary information, Fig. SI-1). We supplemented the list of herbarium records with data from a comprehensive survey of naturalised plants in the Canberra region which used Atlas of Living Australia (https://www.ala.org.au/) records and observations [photos] uploaded to the citizen science website Canberra Nature Map (https://canberra.naturemapr.org/) (Paul Downey and Steve Taylor unpublished data).

The names of naturalised non-native species identified in the Canberra urban area were updated using *Taxonstand* as described above. From our database of the non-native woody species planted in Canberra, we then identified those species recorded as naturalised in the urban area. Naturalised species that were not recorded on our planting list were assumed to have originated from other sources (i.e. they established in the Canberra region through non-horticultural pathways or derived from recent plantings not covered in the dataset, i.e. post 1990) and were excluded from further analysis.

We collected data on plant traits previously linked to naturalisation success for each of the 1439 woody species recorded as planted in Canberra: plant height, seed mass, dispersal mode and cold hardiness. The plant trait data were compiled from several sources but primarily (Mulvaney 1991; Cullen et al. 2011; Duncan et al. 2011). Dispersal mode (obtained from Mulvaney 1991) comprised five categories: wind dispersal (seed/fruit/reproductive unit carried by wind), water dispersal (seed/fruit/ reproductive unit carried by wind), internal animal transport (seed/fruit/reproductive unit carried by animals/birds after digestion), external animal transport (seed/fruit/reproductive unit by animals/birds externally on their body parts, such as hair, fur, feather, foot, horns etc.), and none (species which do not have any specific means of dispersal). We obtained seed mass data (mg) from (Mulvaney 1991). We obtained additional seed mass data from Duncan et al. (2011), Kew Seed Information Database (http://data.kew.org/sid/) and USDA PLANTS (https://plants.usda.gov/java/; USDA, 2008). Data on mean plant height (m) were taken from Duncan et al. (2011).

Canberra experiences cold winters with frequent frosts, so cold tolerance is a factor that could potentially influence naturalisation success. We used hardiness zones to quantify cold tolerance for each species, with the zone data obtained primarily from Cullen et al. (2011), which uses the European Garden Flora (EGF) hardiness zones (Supplementary information, Fig. SI-2). For species not listed in (Cullen et al. 2011), we obtained hardiness zone data from other sources, including CABI (CABI, https://www.cabi.org/), Missouri Botanical Garden (http://www.missouribotanicalgarden.org/), and National Gardening Association (https://garden.org/). When sources used different hardiness zones, we standardised the values to the EGF zones.

Apart from planting effort and introduction period, the remaining plant traits all had missing values for some species. The proportion of the 1,439 species with missing values for each trait were: hardiness zone 6%, plant height 3%; seed mass 47%; dispersal 52% (Supplementary information, Tables SI-2, 3, and 4).

Statistical analysis

We were interested in understanding factors that influenced the probability that non-native woody plant species planted in Canberra had naturalised, so our response variable was whether a species in our planting database had naturalised in the Canberra urban area (1) or not (0). Our analysis involved three steps aimed at untangling the direct and indirect effects of different explanatory variables on naturalisation probability.

First, we separately examined the relationship between each explanatory variable and naturalisation probability to understand the general form of the relationships (univariate analysis). Second, we included all explanatory variables in a multiple regression model to understand their collective influence on naturalisation probability. Third, we used our understanding of the likely ways variables might directly and indirectly affect naturalisation success to fit a path analysis model.

We examined relationships between naturalisation probability (0/1) and each of planting effort, introduction period, seeds mass, plant height, hardiness zone and dispersal mode by fitting logistic regression models. Continuous variables (planting effort, plant height and seed mass) were log10 transformed. Having examined the results from univariate model fitting, we adjusted our explanatory variables to better capture the form of the observed relationships prior to fitting the multiple regression model. Introduction period was treated as a continuous variable taking values 1–8, with 1 being the earliest introduction period or < 1850 and 8 being 1971–1990 (Supplementary information, Table SI-1). We combined hardiness zones H1, H2, H3 and H4 into one category (cold tolerant) and hardiness zones H5, G1, and G2 into a second category (cold intolerant). We reduced the five classes of dispersal mode to three classes: external animal transport and internal animal transport were combined into ‘biotic’, wind dispersal and water dispersal were combined into ‘abiotic dispersal, and unassisted dispersal was kept as ‘none’. For each categorical variable, we specified one category as a reference or baseline class, with the other categories compared to the reference. For dispersal mode, we specified the category ‘none’, and for hardiness zone specified the category ‘cold tolerant’ as the reference class. We then fitted a multivariate logistic regression model with naturalisation probability as the response, all five explanatory variables as fixed effects and plant family as a random effect. For the multivariate model, we standardised the continuous explanatory variables by subtracting the mean and dividing by the standard deviation prior to model fitting.

To handle missing values in the multivariate and path analysis models, we imputed these rather than deleting the incomplete entries. Case-wise deletion would have resulted in a reduced number of species available for analysis, as only 678 of 1,439 species (47%) had complete data for all traits. We modelled missing trait values as a random sample drawn from a distribution of known trait values, with the distribution of trait values for each species comprising the trait values for species in the same family as the species with missing values. For continuous traits (plant height and seed mass) we assumed these were log normally distributed with a different mean and standard deviation for each plant family. Missing categorical data (e.g., dispersal mode and hardiness zone) were modelled as drawn from a multinomial distribution, with the probability of occurrence in each trait category determined by the distribution of occurrences in the family to which the species belonged.

Finally, we fitted a path analysis model to untangle the potential direct and indirect effects of explanatory variables on naturalisation probability, specifically that some species traits could be indirectly associated with naturalisation probability because those traits were linked to planting effort or introduction period. To do this, we identified a path model that described the likely direct and indirect links among explanatory variables (Fig. 1). We then specified and fitted this model, and used the resulting parameter estimates and their uncertainties to measure the relative strengths of the specified pathways.

We fitted all models in a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods implemented in the software JAGS 4.2.0 (Kareth 2016) run through RStudio version 3.3.1 (https://cran.r-project.org/bin/windows/base/old/3.3.1/; Horton and Kleinman 2015). Each model was run using three chains for 10,000 iterations after a burn-in of 5000 iterations, which was sufficient to achieve convergence as measured by the Gelman–Rubin statistic (all values < 1.1; Gelman and Rubin 1992). In addition to plotting the parameter estimates and their uncertainties (95% credible intervals), we used the area under the curve of the receiver operating characteristic (AUC) to evaluate model fit. AUC is a measure of the likelihood that a naturalised species has a higher predicted value from the model than a non-naturalised species, and thus provides a measure of how well the model discriminates naturalised from non-naturalised species across all possible thresholds that could be used to distinguish these classes. An AUC value of 0.5 would indicate a model with no ability to discriminate between the two classes (it performs no better than chance alone), while a value of 1 indicates a model that always correctly assigns naturalised species a higher probability than non-naturalised species. We used the following AUC value interpretations in evaluating model performance: AUC > 0.90 is excellent, 0.90 < AUC > 0.80 is good, 0.80 < AUC > 0.70 is fair, 0.70 < AUC > 0.60 is poor, and 0.60 < AUC > 0.50 is little better than chance (Araújo et al. 2005; Duncan 2016).

Results

In total, 1439 woody plant species were recorded as being planted in Canberra, of which 128 have naturalised (9%).

Univariate analysis

In univariate regressions, the probability of naturalisation increased with increasing planting effort, especially when the index of planting effort exceeded

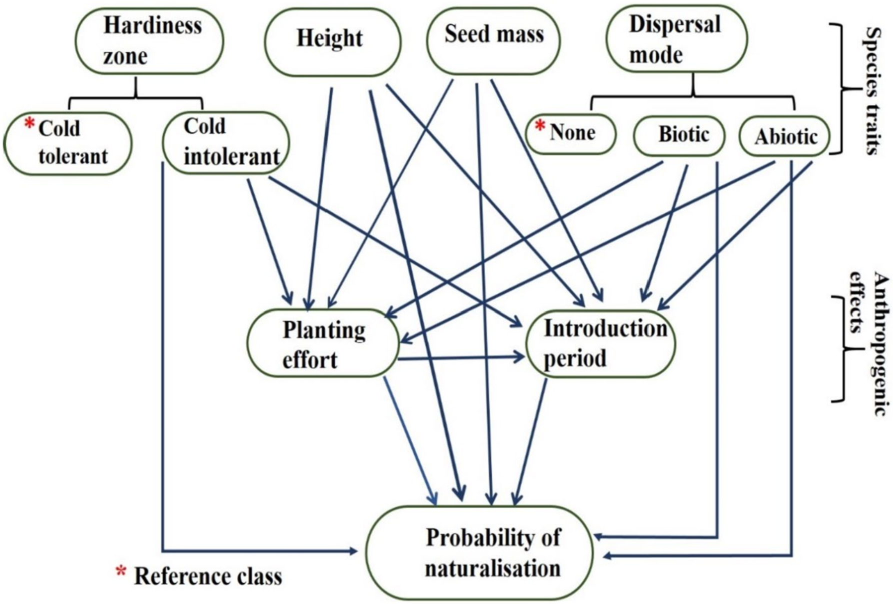

Fig. 1 Full path model showing all the tested relationships (arrows) between species traits and anthropogenic effects (planting effort and introduction period), and probability of naturalisation for woody plant naturalisations. Red asterisks indicate the reference classes for categorical variables (dispersal mode and hardiness zone: see text for details)

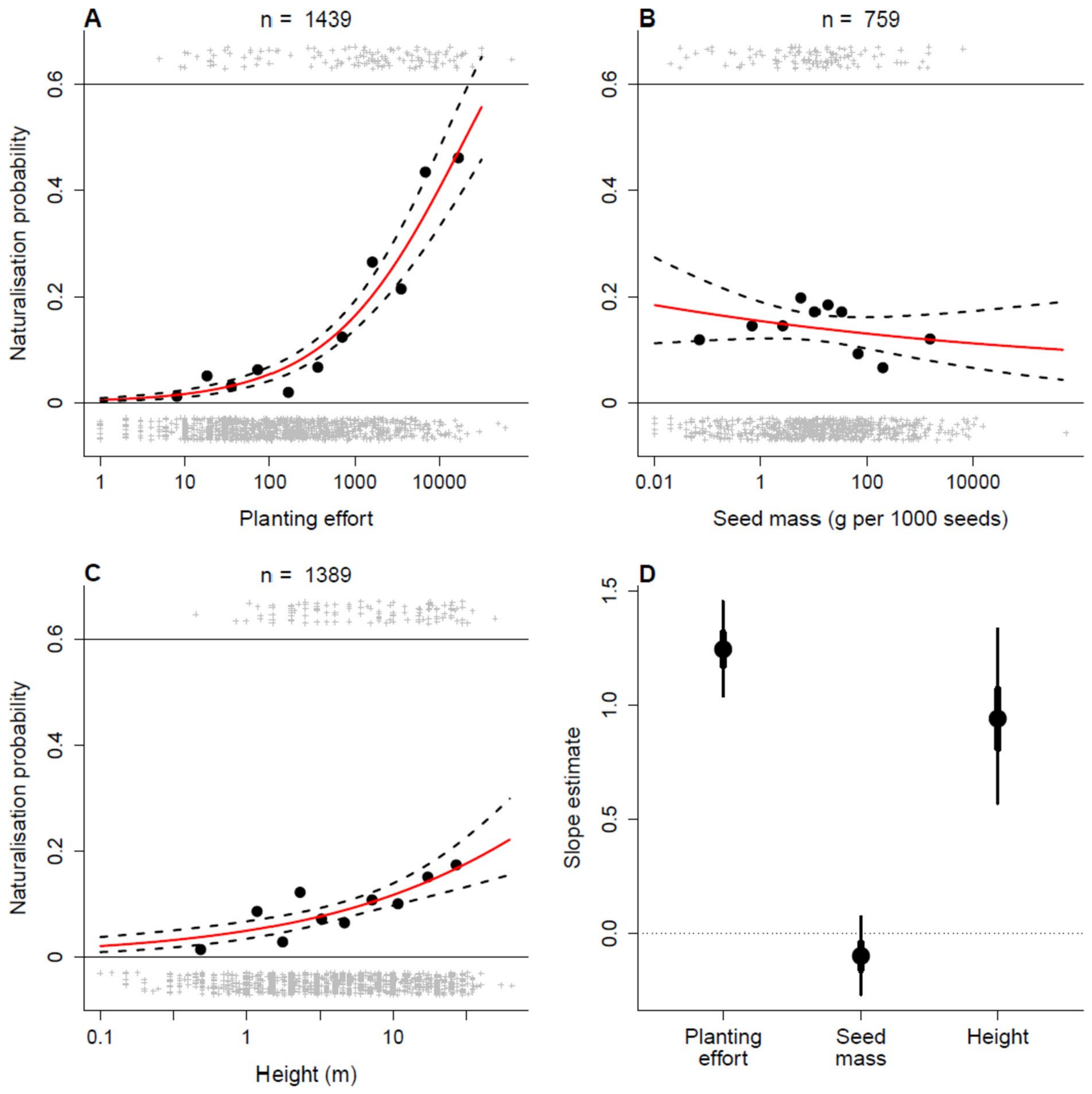

Fig. 2 The relationship between the probability of naturalisation and the continuous variables: **A** planting effort (an index of number of plants planted per species), **B** seed mass, and **C** plant height for woody horticultural plant species planted in Canberra (n = 1439 species) when these variables are included alone in univariate regressions. Grey crosses are the raw data showing either a successful (y-axis values = 1 presented above the grey line) or unsuccessful (y-axis values = 0 presented below the grey line) naturalisation for each plant species. Black dots represent the mean probability of naturalisation for plant species based on approximately even-sized groups of data for each x-axis variable (11 groups for planting effort, 10 for plant height and 10 for seed mass). The red lines are the fitted logistic regression model and the black dashed lines are the 95% credible intervals around the mean model fit. Note: x-axes are log-transformed. **D** the slope estimates (filled circles), and associated 95% and 50% credible intervals (thin and thick lines vertical, respectively) for the relationships shown in (**A**–**C**)

5000, and with greater plant height, but showed no clear relationship with seed mass (Fig. 2). Values where the 95% credible intervals do not overlap zero provide strong evidence that the variables are significantly associated with variation in the probability of naturalisation.

Species able to tolerate temperatures below -5 degrees Celsius (hardiness zones H1, H2, H3 and, H4) had a higher probability of naturalisation than species unable to tolerate those temperatures (Fig. 3a).

Although there was no clear pattern in the relationship between the introduction period and naturalisation probability, in general, species introduced earlier had a higher probability of naturalisation then those introduced later (Fig. 3b). However, naturalisation

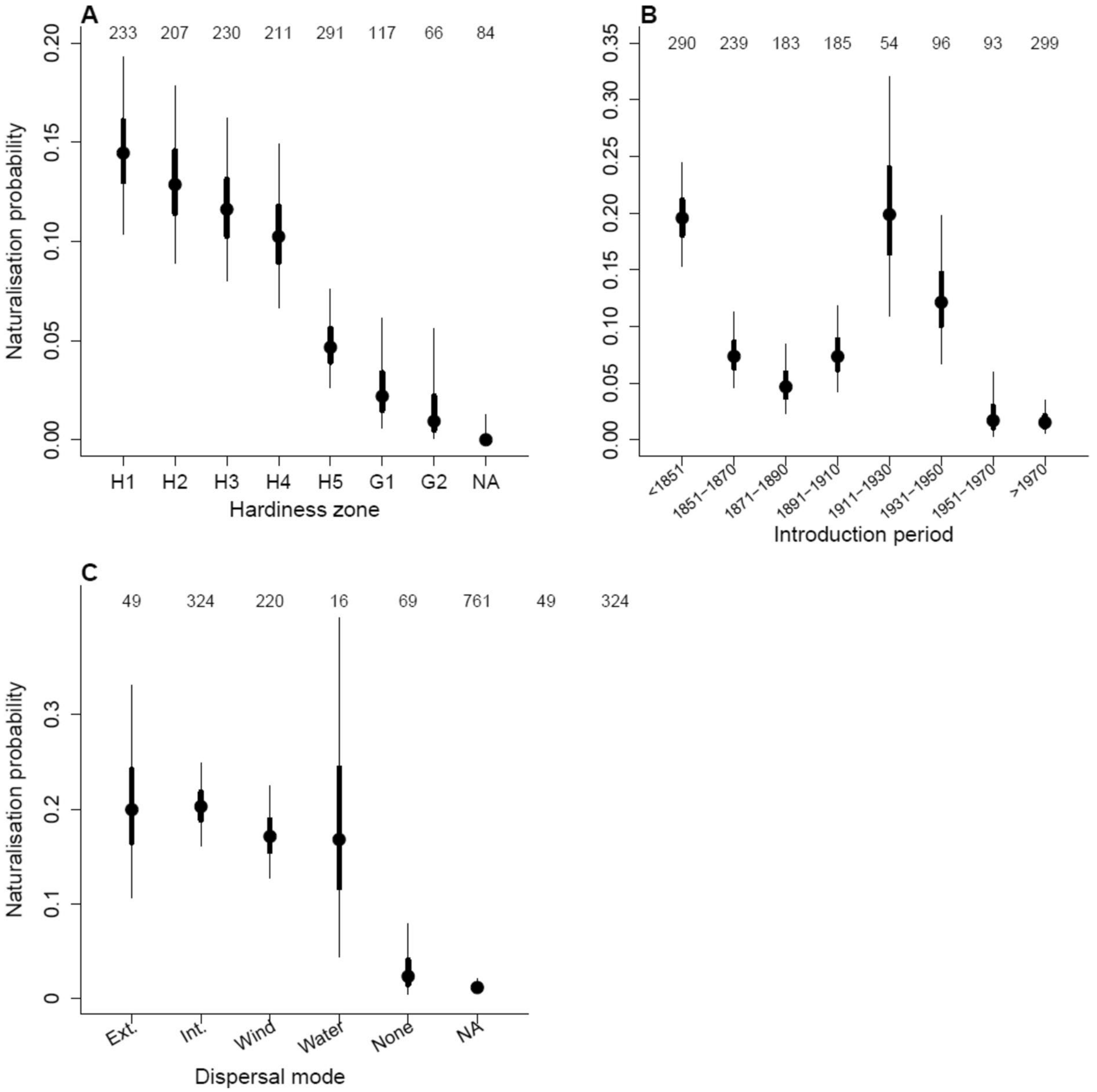

Fig. 3 The relationship between the probability of naturalisation and categorical variables: **A** maximum cold hardiness zone of the woody plant species (from the European Garden Flora), **B** introduction period divided into 8 periods, and **C** dispersal mode for woody horticultural species planted in Canberra (n = 1439) (see text for details). Solid circles show the proportion of species naturalising in each category, lines are the associated 95% and 50% credible intervals (thin and thick vertical lines, respectively). Numbers across the top of each panel show the number of species in each category. NA = species with missing values

probability was unusually high for woody plant species introduced between 1911 and 1930, which could reflect the indirect influence of other variables on naturalisation success. Species introduced between 1911 and 1930, when the city was starting to develop, may have formed the core of plantings, and thus been introduced in larger numbers. Species with obvious dispersal mechanisms had a higher probability of naturalisation than species with no clear means of dispersal (Fig. 3c).

Multiple regression

When all variables were included in a multiple regression model (Fig. 4), naturalisation probability was positively associated with planting effort and plant height, and negatively associated with introduction period and seed mass. In addition, cold intolerant species were less likely to naturalise than cold tolerant species, and species with a clear means of biotic or abiotic dispersal were more likely to naturalise than species with no obvious means of dispersal. The AUC value for the multiple regression model was 0.90, indicating a very strong ability for the modelled variables to distinguish naturalised from non-naturalised species.

Path analysis

The results of the path analysis (Fig. 5) revealed strong direct effects of planting effort, introduction period, seed mass and dispersal mode on the probability of naturalisation. Species with greater planting effort, earlier introduction time, smaller seed mass and a clear means of dispersal were more likely to naturalise. Aside from seed mass and dispersal, other species traits were more strongly linked to naturalisation probability indirectly via planting effort and introduction period. Cold tolerant species, for example, were more likely to be introduced early on and to

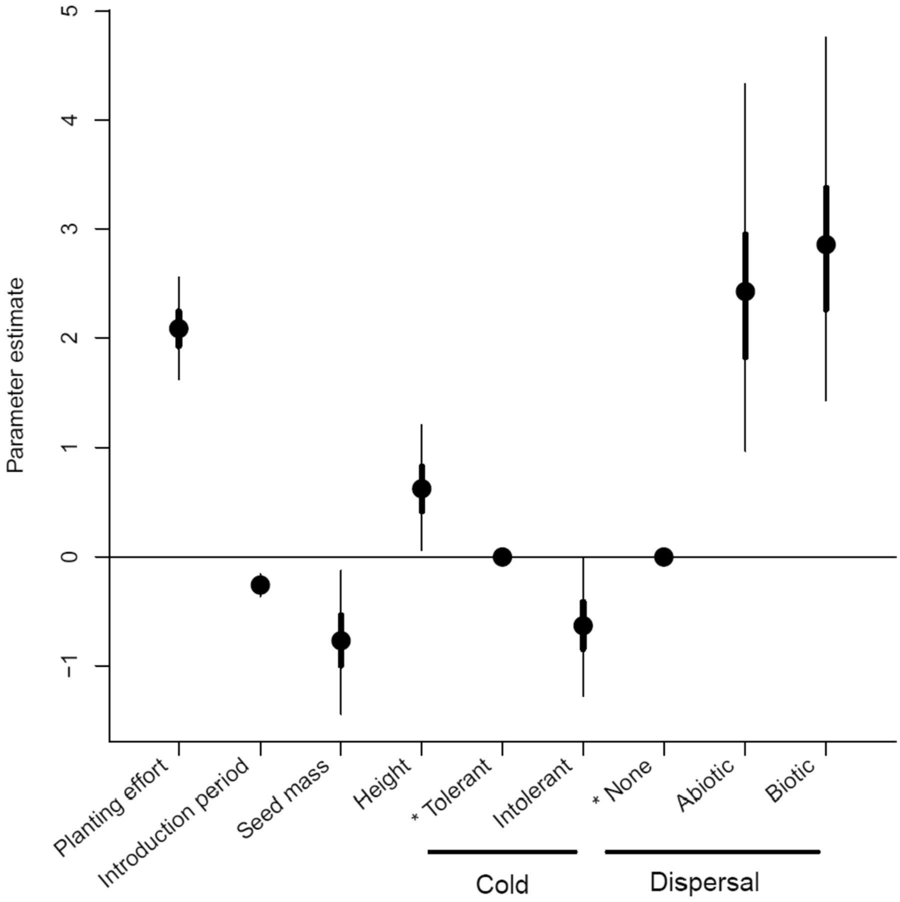

Fig. 4 Multiple regression mean parameter estimates (filled circles) and associated 50% (thick lines) and 95% (thin lines) credible intervals for variables explaining the probability of naturalisation of woody horticultural plants introduced to Canberra. For cold hardiness and dispersal mode, one category (marked with *) was treated as the reference class. Positive (negative) values of the other categories indicate a higher (lower) probability of naturalisation relative to the reference class. Values, where the 95% credible intervals do not overlap zero provide strong evidence that the variables are significantly associated with variation in the probability of naturalisation

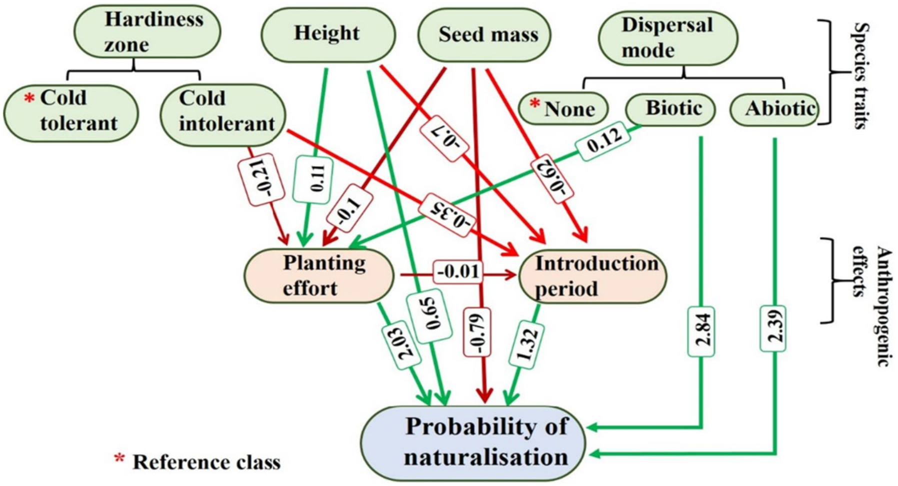

Fig. 5 Path diagram showing the significant relationships between species traits, anthropogenic factors and probability of naturalisation for woody horticultural plants introduced to Canberra. Green solid arrows show significant (95% credible intervals excluded zero) positive relationships and red solid arrows show significant negative relationships. The parameter estimate associated with each significant pathway is shown in the box for each arrow. For categorical variables, one category (marked with *) was chosen as a reference class

be planted in greater numbers, both of which in turn influenced naturalisation probability. Similarly, tall species and those with small seed mass were more likely to be introduced early to Canberra. Dispersal mode had a direct and indirect effect via planting effort on naturalisation probability. Similarly, cold intolerant species tended to have lower naturalisation probability (Fig. 5). Cold intolerant species also had a significant negative relationship with planting effort (parameter estimate = − 0.21). Thus, cold intolerant species were planted in lower numbers than species able to tolerate cold conditions, most likely because of the latter's better match to Canberra's climate. Greater planting effort for cold tolerant species may in turn have facilitated their naturalisation.

Discussion

This study is unique in examining patterns of plant naturalisation in a city with a detailed planting history from the city's inception. The inclusion of species that both naturalised and were introduced but have failed to naturalise provided an opportunity to directly compare the influence of anthropogenic factors and species traits on naturalisation success. Moreover, Canberra's detailed planting records allowed us to quantify the role of planting effort and introduction period in affecting naturalisation success, and to identify how species traits affect naturalisation success both directly and indirectly through relationships with planting effort and the timing of introduction.

As previous studies have found, both planting effort and residence time were strongly related to naturalisation success (Pysek et al. 2009; Maurel et al. 2016): species introduced earlier and planted in greater numbers were more likely to naturalise. Examples of widely planted, early introductions include species introduced for a range of purposes such as *Pinus radiata* (Monterey pine–shelter and timber), *Prunus persica* (peach–ornamental and fruit) and *Hedera helix* (common ivy–ornamental). Here, naturalisation success likely reflects the fact that having more plants in cultivation for a longer period will result in more propagules being released into the environment at a greater number of locations, increasing the likelihood that one or more propagules will encounter conditions suitable to establish a wild population (Mack et al. 2000; Duncan 2021). At the high end of planting effort in Canberra, the probability of naturalisation was high (0.4–0.5; see Fig. 2a). Hence, while the overall probability of naturalisation was ~ 0.09 (128/1439), in accordance with the tens rule proposed by Williamson and Fitter

(1996)—whereby about 10% of introduced species will naturalise—our results suggest this outcome was at least partly shaped by the distribution of planting effort. If more species had been planted in greater numbers, Fig. 2a implies that the naturalisation probability would have been higher. Hence, the tens rule in Canberra appears to be at least partly an outcome of the pattern of human planting preferences.

Residence time, the time since first introduction, is often strongly associated with naturalisation success (Wilson et al. 2007; Pysek et al. 2009; Trueman et al. 2010; Mayer et al. 2017). The present study also demonstrated that the likelihood of naturalisation was highest among plants first introduced in Canberra before 1851 and lowest in plants first introduced after 1970. However, there was a clear increase in naturalisation probability for plants planted between 1911 and 1950 in the univariate analysis (Fig. 3). This rise in the probability of naturalisation coincided with the period when Canberra underwent rapid growth and may reflect an increase in planting effort for species introduced during that period primarily as garden plants. Examples of naturalised species introduced during that period include common ornamental shrubs such as species in the genus *Pyracantha* (firethorns), *Lonicera fragrantissima* (winter honeysuckle) and *Cotoneaster franchetii*. Indeed, when we included residence time as a continuous variable in the multiple regression and path analysis models, we found, having accounted for variation in planting effort, strong evidence for a higher probability of naturalisation for species planted earlier. Species with longer residence time will have had more time to produce a large number of propagules, which in turn likely increases the chance of dispersal and arrival in locations favourable for establishment (Mack et al. 2000; Richardson and Pyšek 2012; Feng et al. 2016). In the case of horticultural species, plants with longer residence time may also be planted more widely, which facilitates naturalisation and spread (Dehnen-Schmutz 2011).

We found that all species traits we examined were at least partly related to naturalisation probability indirectly through relationships with planting effort and introduction period (Fig. 5). This implies that people preferentially selected species with certain traits to introduce early on and to plant in greater numbers, and that these traits were associated with naturalisation success indirectly through links with introduction period and planting effort. In Canberra, taller, cold tolerant plants with smaller seed mass tended to be introduced earlier and planted in greater numbers, which appeared to partly account for relationships between these traits and naturalisation success. Examples include cold tolerant trees such as *Malus domestica* (apple), *Ulmus* (elms) and *Acer negundo* (maple).

Such indirect relationships linked to human preferences are likely to be a feature of plant naturalisation outcomes and one reason it has proven difficult to identify traits consistently linked to naturalisation success. Moreover, these results highlight the critical role that human preferences play in biological invasions and the need to untangle the role of human and biological factors in facilitating the introduction, establishment and spread of species.

Nevertheless, it may still be difficult to identify causal pathways using direct and indirect relationships if there is strong confounding in the data. Cold tolerance was linked with naturalisation success, consistent with the idea that species closely matched to the climate of region they are invading are more likely to establish (Broennimann and Guisan 2008; Beaumont et al. 2009; Feng et al. 2016). Nevertheless, cold tolerance had only an indirect relationship with naturalisation probability: cold intolerant species appeared less likely to naturalise because they were planted in lower numbers and introduced more recently, rather than due to the direct effect of climate matching. But this may not be the case if cold intolerance and planting effort are strongly confounded, which we would anticipate. People would have known that cold intolerant species were less likely to survive Canberra's cold winters, such that cold intolerant species have likely always been planted in low numbers, making it difficult to untangle the causal driver of naturalisation success in this situation. Other traits, including height, seed mass and dispersal mode, may not have been subject to such a strong human planting preference, and indeed all of these traits showed both direct and indirect relationships with naturalisation probability (Fig. 5).

Taller woody plants and those with smaller seed mass and a clear means of dispersal were more likely to naturalise, in part because species with these traits were introduced early on and planted in greater numbers, but also because possessing these traits appeared to directly favour naturalisation success, particularly for dispersal mode. These findings are consistent with other studies that have found associations between these traits and naturalisation success. In general, species with taller stature have greater competitive ability, which may help them compete with the native flora and aid their successful establishment in a new environment (Shipley and Keddy 1994; Pysek et al. 1995). Moreover, previous studies have found a positive effect of plant height on mean seed dispersal distance (Nathan and Muller-Landau 2000; Thomson et al. 2011), which may enable taller plants in cultivation to disperse to a wider range of potential establishment sites. Similarly, both smaller seed mass and a clear dispersal mechanism are features that may aid the spread of propagules to new locations, enhancing the likelihood of naturalisation.

Overall, our findings are consistent with previous studies showing that greater planting effort and longer residence time are particularly strong factors linked to naturalisation success in cultivated plant species. Our findings are also consistent with studies that have identified traits, including cold tolerance, height and dispersal traits, as associated with naturalisation success. What we have shown is that, in Canberra, these species traits appear to be both directly and indirectly linked to naturalisation success, with indirect pathways resulting from human selected species with certain traits for early introduction and greater planting effort. Such direct and indirect pathways are likely to be a feature of most invasion studies, but may be difficult to untangle in studies that use historical data without detailed information on introduction history and planting records.

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Authors contribution R.P., R.P.D., and P.O.D. contributed to the study idea and design. R.P. collected data, performed data analyses with substantial input from R.P.D., and drafted the manuscript with contributions from R.P.D. and P.O.D. All authors discussed the conceptual design and made comments on the manuscript.

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Declarations

Conflict of interest The authors declare no conflict of interest.

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