



Temporal trends in the accumulation of alien vascular plant species through intentional and unintentional introductions in Japan

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Abstract

Clarifying the temporal trends of alien plant accumulation is increasingly important for informing global and national management efforts to decelerate biological invasions, following the adoption of Target 6 of the Kunming-Montreal Global Biodiversity Framework. However, such trends have not yet been analysed in many countries including Japan, which has the highest number of naturalised alien plant species among islands. To clarify the past and recent trends in the accumulation of alien plant species in Japan, we compiled a dataset of the year of first record for 1,463 alien vascular plant species deliberately and accidentally introduced and analysed the changes in the annual number of first records over time for each overall, intentional and unintentional introductions. We found that, overall, the annual number of first records of alien plant species in Japan began to increase in the late 1800s, and the increase continued until the late 1950s, with an estimated maximum of 15.7 new species per year. The increase then halted by 1960 and began a slow decline; the estimated average records per year between 1991 and 2000 dropped to 13.3 species. Since 1900, the annual number of first records associated with intentional introductions has more than doubled the number linked to unintentional introductions. Additionally, the proportion of invasive species brought through intentional introductions was larger than that brought through unintentional introductions. We highlight that while Japan experienced a rapid accumulation of alien plant species, including invasive species, by the 1950s, the rate of accumulation showed signs of saturation by 1960 and has since been slowly declining. Further deceleration and prevention of the introduction of invasive alien species, as targeted in the Kunming-Montreal Global Biodiversity Framework, may be achieved through increased investment in pathway management, especially management of intentional pathways.

Keywords

alien weeds, biological invasion, first record rate, introduction pathways

Introduction

The number of alien species established outside their native range and the associated impacts on biodiversity and human wellbeing have explosively increased in recent centuries due to the acceleration of international trade and travel (Perrings et al. 2005; Westphal et al. 2008; Hulme 2009, 2021; Pyšek et al. 2010; Bonnamour et al. 2021). To avoid further negative impacts, slowing the rate of biological invasions is a pressing global matter (McGeoch et al. 2010; Hulme 2015), as set out in Target 6 of the Kunming-Montreal Global Biodiversity Framework (CBD 2022). Among alien taxonomic groups, vascular plants, which have long histories of utilisation, are one of the largest taxa that have been introduced beyond borders (van Kleunen et al. 2015). In addition to being a threat in itself, the introduction of alien vascular plants has led to additional invasions, because plants are vectors of other non-native organisms such as insects and pathogens (Sikes et al. 2018; Turner et al. 2021). Hence, information on the past and current rates of alien plant accumulation is particularly important for the development of management plans to slow the pace of biological invasions. To date, temporal trends in alien plant accumulation have been estimated at a global scale and at a national scale for several countries in Europe, North America and Oceania (Seebens et al. 2017, 2018) as well as for China (Ni and Deane 2022), and it has been shown that while the global accumulation rate has remained high since the 20th century, national trends have varied, with some countries showing a decline in accumulation rates in recent years (e.g., New Zealand). However, for many other countries, such trends remain unclarified, and it is unknown whether the accumulation of alien plants is continuing or saturated.

Japan is one of the island countries that has the largest number of naturalised alien vascular plant species (Pyšek et al. 2017); nonetheless, there is a lack of analysis of the temporal trends and major pathways of alien plant accumulation. Given that international trade was largely restricted in Japan until 1854 due to a national isolation policy (Asada 2000), the introduction and establishment of alien plants in the country must have proceeded over the following 150 years at a drastic pace involving various intentional and unintentional pathways. Previous studies have documented that intentional introductions, especially those for ornamental purposes, have generally contributed the most to alien plant invasion (Reichard and White 2001; Kowarik 2005). In fact, a global analysis has demonstrated that the majority of the world's naturalised alien species were introduced for ornamental cultivation (van Kleunen et al. 2018). The accumulation of alien plant species in Japan might also be substantially attributable to deliberate, ornamental introduction among various pathways, but this possibility has not yet been verified. Estimating the pace of accumulation of alien plant species in Japan, with its history of national isolation, and identifying the introduction pathways

that have contributed the most to this accumulation will enhance our understanding of global and regional mechanisms of alien plant invasions. Furthermore, doing so will provide an important basis for setting national management goals and targets to decelerate the introduction and establishment of invasive alien species, in line with the Kunming-Montreal Global Biodiversity Framework.

To achieve these goals, in this study, we compiled a dataset of the first record year and introduction pathways for approximately 1,500 alien vascular plant species found in Japan and analysed the changes over time in the annual number of newly recorded species (i.e., first record rates) by pathway throughout the past 150 years. We also calculated the fraction of invasive species brought through each pathway to identify the routes that have contributed the most to the accumulation of problematic alien species with detrimental impacts on biodiversity and human wellbeing. Here, we specifically determine (1) the past and recent trends in first record rates (accelerating, decelerating or saturated) and the period with the greatest first record rates and (2) the pathways through which more invasive species have been introduced and that should be targeted in future management.

Methods

Background information on Japan and its international trade

Japan is an island nation located in East Asia. Historically, the country conducted trade internationally, mainly with neighbouring Asian countries, and with a few European countries, until it was interrupted by the Edo shogunate, the first united government established in 1603 (Asada 2000). The government started prohibiting all international trade except for that with China and the Netherlands in 1639, mainly for religious control. This national isolation lasted over 200 years but officially ended in 1854, when the Japan–US Treaty of Peace and Amity (known as the Convention of Kanagawa) was signed between the United States and the Edo shogunate (Asada 2000). International trade has drastically developed, and Japan's trade partners have diversified since then (Yamazawa and Yamamoto 1979), creating more opportunities for biological invasions. Japan experienced dramatic economic growth after World War II ended in 1945, and international trade further expanded (Trade Statistics of Japan, https://www.customs.go.jp/toukei/suii/html/nenbet.htm). Complied long-term trade data show that the annual import value in 1950 was 15 times that in 1940, and this value has continuously increased since then to the present (Suppl. material 1).

Compilation of data on alien plant species

We generated a dataset on alien vascular plant species introduced from overseas to Japan using the following four steps. First, we created a list of alien plant species based on Yonekura (2012), a comprehensive plant inventory that enumerates the standardised scientific names and Japanese names of approximately 11,000 alien and native vascular

plant species recorded in the Japanese archipelago. From Yonekura (2012), we extracted all alien species, infraspecific taxa such as subspecies and varieties, and hybrids (hereafter referred to as species for simplicity) that have naturalised (i.e., maintained self-sustaining populations) and those that have not yet been confirmed to have naturalised but are frequently observed to escape cultivation. We restricted our listing to alien species that the literature clearly identified as naturalised or escaped, and we excluded species described as "possibly" naturalised or escaped to ensure data quality. The resulting list included a total of 1,753 species. Although the species names extracted from Yonekura (2012) for our list did not entirely correspond to the names accepted in international taxonomic sources such as The WFO Plant List (https://wfoplantlist.org/plant-list/), they were considered widely referenced in Japan. Therefore, we used the species names in the list (for taxa below the species level, those including infraspecific epithets) as a standard against which to standardise species names reported in other information sources. The standardisation was conducted referring to Ylist (http://ylist.info/index. html), a web-based nomenclatural index of names of vascular plants in Japan, which was created by the same author as Yonekura (2012) and follows the same taxonomy.

Second, we gathered information on the year of first record of each listed species from four comprehensive illustrated reference books on alien or cultivated plant species in Japan: Honda et al. (1988a, b, c, d), Shimizu et al. (2001), Shimizu (2003) and Uemura et al. (2010). If the year of first record was shown as a period such as the "1950s" or "Meiji era", the middle year of the term was employed. Similarly, if the year was provided as the "early", "late" or "end" of a certain period, we applied "first year of the period + 1", "the middle + 1" or "the last year - 1", respectively (for example, 1991 for "early 1990s"). In cases where there was an inconsistency in the years among the literature, the oldest was employed. Based on the four reference books, we identified the year of first record for 48% of species on the list. To fill the data gap, we further referred to the Science Museum Net (https://science-net.kahaku.go.jp/, accessed in June-August 2022), a database of specimen records kept in more than 80 natural history museums across Japan (Hosoya et al. 2018). From the database, we extracted the collection year of the first (i.e., oldest) specimen of the species, which allowed us to increase the proportion of listed species with the year of first record to 86%. We also collected information on the year of introduction, where possible, from the four illustrated books described above and an encyclopaedia on the history of plant cultivation in Japan (Shimizu 1984) to identify species that were introduced before 1603, when the Edo shogunate was established and literacy rates began to increase (Saito 2012). The reason is that it is highly likely that those archaeophyte species were discovered but not recorded in written form before the year of first record collected from the books or specimens and therefore should subsequently be excluded from analysis. Information on the year of introduction was used only to identify archaeophyte species and was not incorporated into the analysis.

Third, we compiled information on the introduction pathways of the listed species or descriptions of how the species was used as a surrogate for the introduction pathway. We applied a major pathway classification, i.e., intentional and unintentional. We further classified them into pathway categories defined by the Convention on Biological

Diversity (CBD 2014) but only employed release in nature and escape from confinement as intentional pathway categories and contaminant and stowaway as unintentional pathway categories. Corridors and unaided spread categories were not relevant, considering the geographical conditions of Japan as an island nation. As the number of species associated with escape from confinement was substantially large, we subdivided this category into six subcategories, taking into account the conditions of plant cultivation in Japan (Suppl. material 2), i.e., escape from agriculture, botanical gardens, food for pets, medicinal and industrial purposes, ornamental purposes and research, which are partially compliant with the CBD subcategories detailed in Harrower et al. (2020). As the source of information on introduction pathways, we first consulted the four illustrated reference books described above and then further referred to most of the available literature specifically including a list of unintentionally introduced alien species in Japan (Japan Forage Crop Seeds Association 1972; Murayama et al. 1989a, b; Asai et al. 2007, 2009; Shimono and Konuma 2008; Ikeda et al. 2022). The reason is that unlike intentional introductions, unintentional introductions are often not recorded (Lehan et al. 2013) and, as a result, may be incompletely presented in the illustrated reference books. For each species, we recorded all pathways for which evidence was available, not only one main pathway. The species for which no information on introduction pathways was found in any of the literature were grouped as species of unknown pathways.

Finally, we compiled information on whether each species has been recognised by the Japanese government as harmful to biodiversity and human wellbeing by referring to two invasive alien species lists created by government agencies, one made in 2005 ("the alien species alert list", Ministry of the Environment 2005) and the other made in 2015 ("the list of alien species that may have adverse effects on ecosystems in Japan", Ministry of the Environment and Ministry of Agriculture, Forestry and Fisheries 2015). The alien species on the lists were selected based on their impacts on native species, ecosystems, human health and economic activities (Ohsawa and Osawa 2014; Egawa and Matsuhashi 2022). Although these lists are not legally binding in themselves, they have been developed to identify and raise public awareness of harmful species that need to be managed. In the present study, we defined invasive alien species as species included on one or both of the government lists, i.e., species that have serious impacts and a recognised need for management at a national level.

The compiled dataset included 46 archaeophyte species that were introduced before 1603, and we removed those species to ensure data quality. Doing so resulted in 1,707 species left for analysis, of which 1,463 species had information on the year of first record.

Data availability

The dataset generated during this study is considered the largest of first records for alien vascular plant species in Japan, given that the number of alien vascular plant species tagged with Japan currently registered in the Alien Species First Records Database (Seebens 2021) is 165. The dataset is available at https://doi.org/10.5281/zenodo.7597598 (Egawa and Koyama 2023).

Data analysis

All data analyses were performed using the R statistical environment (R Core Team 2020). The cumulative number of first records throughout was calculated for each overall, pathway category and subcategory, using data on 1,463 species with information on the year of first record. First record rates (i.e., annual number of species newly recorded) were also calculated for overall and each of the same pathway groups as above. To check the association between the first record rate and trade value, the correlation between the overall first record rate and annual import value was tested using Spearman's rank correlation coefficients (Suppl. material 1).

The temporal trends of the first record rates were modelled using generalised additive models (GAMs) in the mgcv R package. The GAMs enabled us to illustrate nonlinear trends over time. Because of the nature of first record rates as overdispersed count data, we applied a negative binomial distribution with a log link function. In addition to the overall trend without distinguishing introduction pathways, a separate model was constructed for each pathway category and subcategory having a sufficient sample size, which is here defined as more than 40 species. The theta parameters of negative binomial distributions were estimated during model fitting. If the relationship between time and the first record rates was not significant at p < 0.05 for a given pathway according to the GAM, we considered that the first record rates associated with the pathway did not change temporally. In our dataset, the first records of alien plant species before 1845 were found in only three fragmentary years (1699, 1735 and 1784), and the number of recorded species in these three years was limited to five. Likewise, first records after 2000 (110 species) were possibly underrepresented due to the delay between observation and report, as seen in the sharp decline in the number of first records in the last 20 years (Suppl. material 1: fig. S1-2B). Therefore, we restricted our GAM analysis to 1,348 species for which the first record years were identified between 1845 and 2000.

To determine the pathways responsible for the accumulation of invasive alien species, we tested whether the proportion of invasive species to all species introduced through each pathway differed from the overall pattern without distinguishing pathways using Fisher's exact test with Bonferroni correction of p values in the RVAideMomoire R package. We considered pathways with a significantly higher proportion of invasive species than the overall pattern as more responsible in terms of invasive species introduction. The analysis was conducted only for pathways involving more than 40 species.

Results

Temporal changes in cumulative number and first record rate of alien plant species

The cumulative number of first records of alien plant species in Japan has been increasing since the late 1800s due to both intentional and unintentional introductions and largely due to introduction through unknown pathways (Fig. 1A). Among the

intentional pathways, escape from ornamental uses contributed the most to the accumulation of new species, followed by escape from agriculture, throughout the investigation period (Fig. 1B). For unintentional pathways, the contribution of contaminants was far greater than that of stowaways throughout the investigation period (Fig. 1C).

The GAM analysis detected significant temporal trends in first record rates during the period from 1845 to 2000 for overall and all the examined pathways except for release in nature (Fig. 2, Suppl. materials 3, 4). The overall first record rate of alien plant species in Japan began to accelerate in the late 1800s and continued until the late 1950s, with an estimated maximum of 15.7 new species per year during the period from 1955 to 1960 (Fig. 2A). Since 1961, the first record rate has slowly decelerated (Fig. 2A); the model-estimated average annual first record rate during the recent 10-year period from 1991 to 2000 was 13.3 species. Spearman's correlation coefficients showed that the overall first record rates had been significantly associated with the annual import value approximately 10 years earlier until 1950, but the association with the import value disappeared after 1960 (Suppl. material 1). The GAM-estimated temporal trends of first record rates of intentional and unintentional introductions were also of a onepeak type, although the timing of the peak differed between pathways. The first record rate associated with intentional introduction peaked at 5.6 new species per year around 1940 and started to decelerate from 1946, averaging 3.2 species per year in recent years from 1991 to 2000 (Fig. 2B). This pattern was largely attributable to the patterns of two main intentional pathways, escape from ornamental uses, with a maximum of 3.7 species per year in the 1940–1947 period, and agriculture, with a maximum of 1.5 species per year in the 1931-1942 period (Suppl. material 4). The first record rate associated with unintentional introduction, which was mostly attributable to contaminants, peaked around 1945, with an estimated maximum of 2.4 new species per year, and started slowing around 1950 (Fig. 2C). The average first record rate through unintentional introduction in the recent 10-year period was estimated at 1.4 species per year. Compared to intentional and unintentional introductions, the first record rate relevant to unknown introduction peaked later, i.e., around 1965, with an estimated maximum of 9.4 species per year. The rate remained largely unchanged until 2000 (Fig. 2D).

The proportion of invasive species by pathway

The proportion of invasive species to all species varied across introduction pathways (Fig. 3). Compared to the overall pattern not distinguishing pathways (11%, 193 in 1,707 species), the proportion of invasive species brought through intentional introductions was significantly higher (20%, 109 in 549 species; p < 0.001, Fisher's exact test with Bonferroni correction). Three intentional pathways, i.e., escape from ornamental and agricultural purposes and release in nature, showed significantly higher proportions of invasive species than the overall pattern (Fig. 3; p < 0.05). In contrast, the proportion of invasive species brought through unknown pathways was significantly lower (6%, 65 in 1,022 species; p < 0.001) than the overall proportion. The proportion of invasive species introduced through unintentional pathways (18%, 40 in 220 species) did not statistically differ from the overall pattern (Fig. 3; p = 0.205).

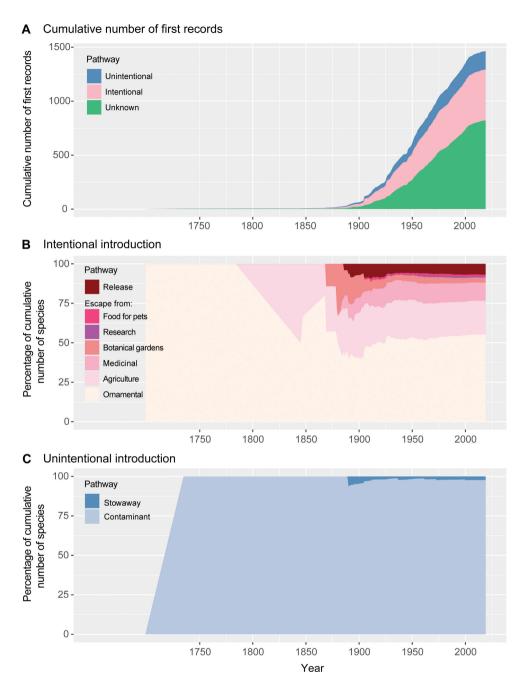


Figure 1. Cumulative number of alien plant species by introduction pathway in Japan **A** cumulative number of first records **B, C** percentage of species introduced by each pathway in the cumulative number of species introduced via intentional and unintentional introductions, respectively.

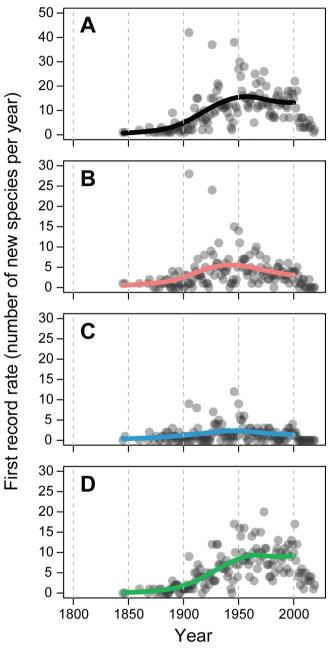


Figure 2. Temporal trends in first record rates in Japan, 1845–2000 **A** overall trends without distinguishing pathways **B–D** trends for intentional, unintentional and unknown introductions, respectively. Grey dots indicate the observed numbers of first recorded species, and lines indicate the generalised additive model (GAM) estimations (for the model fitting results, see Suppl. material 3). Note that the observed numbers of the first recorded species after 2000 are shown for reference purposes but were not included in the GAM analysis.

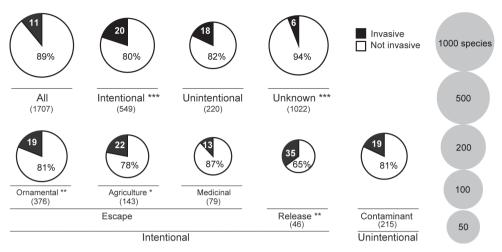


Figure 3. Proportion of invasive species by pathway with more than 40 species involved. Asterisks indicate significant differences in the proportion of invasive species compared to the overall pattern (All) without distinguishing pathways (Fisher's exact test with Bonferroni correction of p values: * p < 0.05, ** p < 0.01, *** p < 0.001). The numbers in brackets and size of the pie charts show the total number of species involved in the pathways. As one species may be included in multiple pathways, the number for each subcategory amounts to more than the overall number (All).

Discussion

Our analysis using a newly compiled dataset yielded the following two key findings on the temporal trends and main pathways of alien plant accumulation in Japan: (1) starting in the late 1800s when the country opened its borders, the accumulation of alien plant species accelerated, but by 1960, the pace of accumulation showed signs of saturation and has been slightly decreasing since then to the present. (2) The accumulation of invasive alien species with detrimental impacts on biodiversity and human wellbeing is largely attributed to intentional introductions, including those for ornamental purposes, as well as agricultural purposes and release in nature.

Our estimation of the maximum overall first record rate in Japan, 15.7 new alien plant species per year, was 1.8 times the maximum rate of 8.8 species per year recorded in China in the early 1900s (Ni and Deane 2022). Similarly, the maximum first record rate that we obtained was greater than the peak rates estimated in a previous study on other islands, such as the United Kingdom and the Hawaiian Islands (Seebens et al. 2017). Given that we collected the year of first record for only 86% of the species in the compiled list, the actual first record rates in Japan should be even greater than the estimation shown here. Such an intensive accumulation of new species would have led to the largest number of naturalised alien plant species in Japan among island nations.

However, we found that the overall first record rate peaked in 1955 and slowly began to decline in 1961. This saturation and subsequent decline are possibly due to multiple social and environmental factors. For example, the reduced access to new alien species pools because of the saturation of the diversity of trade partners can lead

to a slowdown of the first record rate (Seebens et al. 2015, 2018). This process may be relevant to Japan because although Japan's import partners diversified immediately after the opening of the country, the North American share stayed high, especially after World War II ended in 1945 (Yamazawa and Yamamoto 1979). Another possible explanation is increased biosecurity efforts. Japan enacted the Plant Protection Act in 1950 and enforced a systematic import quarantine of vascular plant species that may carry plant pests and diseases (Sakata 2011). Additionally, since 1967, Japan has participated in the Organisation for Economic Co-operation and Development (OECD) Schemes for the Varietal Certification of Seed to ensure the use of high-quality agricultural seeds with reduced contamination risk. These import-related biosecurity efforts may have contributed to the recent slowdown of the first record rate since 1961. These explanations are also consistent with the results of correlation analysis showing that after 1960, the association between the first record rate and import value disappeared, with the annual number of newly recorded species not increasing even as import value increased (Suppl. material 1). In addition to these factors, temporal changes in land use and environmental suitability due to climate change might be involved in the saturation of first record rates, as suggested by previous studies (Walther et al. 2009; Seebens et al. 2021). All factors are not mutually exclusive and could thus have contributed interactively.

As above, we found a promising tendency in which, overall, the accumulation of new alien plant species in Japan has been saturated and even slowing despite the continuing trade expansion. Nonetheless, the estimated first record rate in the recent 10-year period from 1991 to 2000 was still more than 13 species per year. Based on the proportion of invasive species to all introduced species (11%), the first record rate of 13 new species per year implies that at least one novel invasive species is included every year. We found that the first record rate via intentional introduction exceeded the rate via unintentional introduction throughout the study period. This finding is in line with previous studies highlighting the primary roles of intentional introduction in alien plant invasion (Lonsdale 1994; Hulme et al. 2008). In particular, escape from ornamental horticulture is known as the major introduction pathway for non-native species in Europe and regions with cultural legacies of European colonialism (Lehan et al. 2013; van Kleunen et al. 2018). Our results showing the importance of intentional introduction, especially for ornamental purposes, in the accumulation of new species are in line with this pattern, although Japan historically has a different cultural sphere from Europe. We also found that intentional introductions are even responsible for the introduction of invasive species, specifically defined here as species on the government's alert lists for their detrimental impacts on biodiversity and human wellbeing. Similarly, in China, 50% of invasive alien plant species were intentionally introduced for various purposes (Xu et al. 2006). These results suggest that, in line with the global direction (Perrings et al. 2005), managing intentional introductions is key to reducing the accumulation of invasive alien plant species in East Asia. In the present study, information on specific introduction pathways was not found for 60% of all listed species. We assume that the majority of the species with unknown pathways were unintentionally

introduced as contaminants or stowaways because intentional introductions of species are more likely to be recorded (Lehan et al. 2013). Therefore, in this study, species associated with unintentional introductions are presumably underrepresented. However, the possible underestimation of unintentionally introduced species does not affect the implication of the study that the management of intentional introduction holds particular importance for slowing the accumulation of invasive species in Japan. The reason is that the proportion of invasive species brought through unknown pathways was much smaller than that brought via other pathways. Hence, combining data on species with unknown pathways does not increase the fraction of invasive species brought through unintentional introduction.

Conclusion

This study demonstrated the long-term trend of alien vascular plant accumulation in Japan and the introduction pathways that have most contributed to the accumulation. We believe that the results of this study could be a basis for developing national policies and action plans to achieve Target 6 of the Kunming-Montreal Global Biodiversity Framework, which aims to reduce the rates of introduction and establishment of invasive alien species by at least 50% (CBD 2022). If the first record rate of alien vascular plants was to be reduced by half in Japan, based on our estimation of the recent 10-year period from 1991 to 2000, the rate should be cut to at least 7 new species per year. Further investments and efforts in pathway management, especially the management of intentional pathways, will be needed to achieve this rate, but they will ultimately contribute to eliminating the impacts of invasive alien species and conserving biodiversity and human wellbeing.

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Supplementary material I

Association between the first record rate and import value

Authors: Chika Egawa, Asuka Koyama

Data type: text including figures and a table (PDF file)

Explanation note: Methods and results of testing the association between the first record rate and import value.

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Link: https://doi.org/10.3897/neobiota.83.101416.suppl1

Supplementary material 2

Definitions of subcategories used for escape from confinement

Authors: Chika Egawa, Asuka Koyama

Data type: table (PDF file)

Explanation note: Definitions of subcategories used for escape from confinement in

this study.

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Link: https://doi.org/10.3897/neobiota.83.101416.suppl2

Supplementary material 3

Generalised additive model (GAM) results

Authors: Chika Egawa, Asuka Koyama

Data type: table (PDF file)

Explanation note: Generalised additive model (GAM) results of the temporal trends

in the first record rates.

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Supplementary material 4

Temporal trends in first record rates from 1845 to 2000 by subcategory of introduction pathway

Authors: Chika Egawa, Asuka Koyama

Data type: figure (PDF file)

Explanation note: Temporal trends in first record rates from 1845 to 2000 by subcategory of introduction pathway.

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