Relative importance of biological and human-associated factors for alien plant invasions in Hokkaido, Japan

Running title: Factors associated with plant invasion success

Relative importance of biological and human-associated factors for alien plant invasions in Hokkaido, Japan

Chika Egawa [1,*], Takeshi Osawa[1,2], Tomoko Nishida[3], Yasuto Furukawa[4]

[1] Institute for Agro-Environmental Sciences, National Agriculture and Food Research Organization, 3-1-3 Kannondai, Tsukuba, Ibaraki, 305-8604, Japan

[2] Current address: Faculty of Urban Environmental Sciences, Tokyo Metropolitan University, 1-1 Minami-Osawa, Hachioji, Tokyo, 192-0397, Japan

[3] Headquarters, National Agriculture and Food Research Organization, 3-1-1 Kannondai, Tsukuba, Ibaraki, 305-4517, Japan

[4] Rakuno Gakuen University, 582 Bunkyodai-Midorimachi, Ebetsu, Hokkaido, 069-8501, Japan

* Corresponding author (C. Egawa)

Email: cegawa@affrc.go.jp

Tel: +81 29 838 8271

Fax: +81 29 838 8271

Abstract

Aims

The invasion success of alien plants is strongly affected by both biological and human-associated factors. Evaluation of the relative contribution of each factor is important not only for the further understanding of invasion processes but also for the better management of invasion risk, particularly in protected areas of high conservation priority. Here, we quantified the relative importance of species biological traits and association with a human activity, i.e., agriculture, in explaining the invasion success of alien plants across the entire region and in protected areas in Hokkaido, Japan.

Methods

As a quantitative measure of invasion success, the distribution extent of naturalized populations across the entire prefecture and in protected areas was calculated for 63 alien species with equal residence time based on species occurrence records at a spatial resolution of 5-km mesh grid units. For each species, we identified seven biological traits (seed mass, dispersal mode, maximum plant height, capability of vegetative reproduction, flowering start time and period, and life span) and two human-associated factors (introduction purpose and cultivation frequency for agricultural use). Cultivation frequency was determined based on the frequency of seed-sowing in pastures: 1. not sown, 2. accidentally sown as a seed contaminant, and 3. intentionally sown for commercial cultivation. The importance of biological traits and human-associated factors in explaining the distribution extent was determined using an information-theoretic approach.

Important Findings

In explaining the distribution extent across the entire prefecture, species biological traits and human-associated factors showed comparable importance; cultivation frequency exhibited the highest importance value closely followed by seed mass, maximum height, and flowering period. In contrast, when focusing on protected areas, human association was more important than biological traits, as indicated by the greatest importance of cultivation frequency and much lower values for most biological traits. The results demonstrated that species biological traits and human association almost equally contributed to invasion success across the entire region, while invasions into protected areas were more attributable to human association than to biological traits. We highlight that the control of propagule pressure associated with artificial cultivation may be key to preventing further invasions into protected areas.

Keywords: agricultural use, biological invasion, distribution, nature reserve, pasture plants

Introduction

The introduction of alien plant species that can spread in natural habitats still continues or has even accelerated worldwide (Seebens *et al*. 2017). Clarifying the mechanisms determining invasion success is a pressing matter for managing the risk of alien plants (Groves *et al*. 2001). The invasiveness of alien plants is largely determined by the biological traits of species (Rejmánek *et al*. 2005), of which several have been found to promote invasion. For example, the capability of vegetative reproduction is often advantageous for invasion success because vegetative reproduction promotes rapid range expansion in new sites where breeding mates are absent (Pyšek and Richardson 2007; Drenovsky *et al*. 2012). In addition to the biological traits of species, recent studies have emphasized that association with human activity must be considered when explaining the invasion success of alien plants (Thuiller *et al*. 2006; Dehnen-Schmutz *et al*. 2007; Gravuer *et al*. 2008; Maurel *et al*. 2016) because species that are involved with economic activities, such as agriculture and horticulture, are often conferred a propagule-pressure advantage and are thus more likely to succeed in establishing and spreading in landscapes than species with no relations (Lonsdale 1994; Lockwood *et al*. 2005; Shimono and Konuma 2008). However, although the influences of both biological traits and human association on alien plant invasions are obvious, the extent to which each factor contributes remains an open question. Assessments of the relative importance of biological and human-associated factors in invasion success are necessary to further understand the invasion mechanisms of alien plants.

From a conservation perspective, clarification of the mechanisms of invasion in protected areas is of particular interest because the establishment of alien species is most problematic in protected areas, where the conservation of native biodiversity is mandated (Foxcroft *et al*. 2013). Protected areas generally maintain natural vegetation with fewer anthropogenic disturbances, and because many alien species fail to establish without artificial disturbances that increase resource availability (Rejmánek *et al*. 2005; Colautti *et al*. 2006), the invasibility of vegetation in protected areas is potentially lower than that of vegetation in surrounding areas, including those subjected to human disturbance (Rose and Hermanutz 2004; Pauchard *et al*. 2013). Considering the low invasibility of the involved vegetation, it is probable that the relative importance of species biological traits and human association in determining invasion success in protected areas differs from the general patterns covering the entire area in the region. Specifically, human association may play a more important role than species biological traits in invasions into protected areas because an extrinsic supply of propagules is vital for the invasion of areas with environmental resistance (Simberloff 2009), whereas such a supply may not be essential for successful invasion into disturbed vegetation outside protected areas. Evaluation of the relative contribution of species biological traits and human association to invasion success in protected areas and across entire regions, including disturbed areas, will provide essential information for understanding general and protected-area-specific invasion mechanisms and potentially effective management solutions for alien plants.

Here, we quantified the relative importance of species biological traits and association with human activity to the invasion success of alien plants in protected areas and across the entire region of Hokkaido Prefecture, northern Japan, using distribution extent as a quantitative measure of invasion success (Wilson *et al*. 2007; Pyšek *et al*. 2011; Akasaka *et al*. 2012). As a human activity that can promote alien plant invasions, we considered agriculture because it is the means by which large numbers of alien plant species are introduced and distributed into novel locations (Lonsdale 1994; Driscoll *et al*. 2014; Overholt and Franck 2017). In Hokkaido, grassland-based dairy farming has been very common, and many pastures are adjacent to nature reserves (Egawa 2017). Therefore, we expected that association with pastoral agriculture would be an important factor in explaining the invasion success of alien plants in protected areas as well as the entire area of the prefecture, so we incorporated two agriculture-related variables, i.e., introduction for the purpose of agricultural use (representing the association at the time of introduction) and cultivation frequency (representing the association after the introduction). We specifically asked the following questions: What is the relative importance of biological and human-associated factors in determining invasion success in protected areas and across the entire prefecture, and what are the main factors that should be managed to prevent further invasions into protected areas?

Materials and methods

Study site

Overview of Hokkaido

The study site, Hokkaido, is the northernmost prefecture in Japan and consists of one main island and several small islands, with a total area of 8,345,000 ha (Fig. 1a). The climate in Hokkaido is categorized as a temperate subarctic climate with an annual precipitation of 800–1500 mm and an annual mean temperature of 6–10°C (Matsushita *et al*. 2004).

Hokkaido Prefecture remained largely unexplored until the beginning of the land development effort led by the Meiji government in 1869 (Japan Livestock Industry Association 1976). Since that time, the land was gradually developed, but the area of pastures was less than 65,000 ha, which was 0.8% of the whole Hokkaido area, as of 1960 (Hokkaido Agricultural Experiment Station 1973). Large-scale, intensive pasture development in Hokkaido began in the 1960s, which dramatically increased the area of pastures (Japan Livestock Industry Association 1976), although unprofitable pastures were often abandoned (Hokkaido Regional Development Bureau 1967; Tateishi 1985). As of

2005, pastures occupied 515,900 ha, constituting 6% of the whole Hokkaido area.

By the end of the Meiji era in 1912, more than 50 alien plant species had been intentionally introduced to Hokkaido for use in pastoral agriculture (Nishimura 1988), although many were recognized as unsuitable and not used for commercial cultivation (Japan Livestock Industry Association 1976). Since 1914, the Hokkaido government has regularly designated well-qualified species as recommended based on the results of cultivation trials and has encouraged their cultivation. Most species that have been commercially cultivated to date were the government-recommended species introduced during the Meiji era, although the introduction of pasture plants continued after this period.

Hokkaido currently has six national, five quasi-national, and 12 prefectural nature parks, in which several types of nature reserves have been established to conserve native landscapes and biodiversity. Among all the types of nature reserves, the special protection areas and the first type of the protection areas (hereafter, these two reserve types are collectively called protected areas) are considered the most important territories with the highest conservation priority and are protected by the strictest regulations. Protected areas account for 3.6% of the total area of Hokkaido. As commonly found in various countries (Meiners and Pickett 2013), nature parks in Hokkaido lie within a matrix of human-disturbed land and some are directly adjacent to pastures (Egawa 2017).

Vegetation across the entire area and in protected areas in Hokkaido

According to the vegetation map from 1999 created by the Ministry of the Environment of Japan (the associated GIS data are available at http://gis.biodic.go.jp/webgis/sc-025.html?kind=vg Accessed 26 Jul 2017), the percentages of human-disturbed vegetation (including urban areas, agricultural land, secondary forest and grassland, and planted forest), natural vegetation (including wet and dry grasslands and forest) and other areas (including open water areas) across Hokkaido are 46.9%, 45.3%, and 7.8%, respectively (Table S1). Heavily disturbed areas, i.e., urban areas and agricultural land, account for 20.5% of the whole prefecture. On the other hand, most protected areas consist of natural vegetation (84.7%), and the percentage of human-disturbed vegetation is small (2.8%). Other areas including open water occupy 12.4% of the total protected areas. Most of the human-disturbed vegetation in protected areas is secondary grasslands and forests, and the percentage of urban areas and agricultural land is 0.1% of the total protected areas (Table S1).

Study species and their distribution data

We limited our study species to those introduced (either intentionally or accidentally) to Hokkaido during the same period, i.e., the Meiji era from 1869 to 1912, to eliminate the effects of residence time, and we focused on identifying the influences of species biological traits and human association. Candidate species were identified based on Nishimura (1988) and Igarashi (2001). Only herbaceous species were considered since there were very few tree species introduced during the Meiji era (Igarashi 2001). Because nearly 100 years have passed since their introduction, candidate herbaceous species likely had sufficient time to expand their distribution ranges in Hokkaido. The plant nomenclature was based on YList (http://ylist.info Accessed 29 Jan 2017).

To estimate the distribution extent of alien species, we used occurrence records at a spatial resolution of 5-km mesh grid units (the Five-Fold Mesh) in the Hokkaido Blue List (BL) alien species database (http://bluelist.ies.hro.or.jp/ Accessed 1 March 2017; Fig. 1b). The occurrence records in the BL database were compiled from 44,833 observations of naturalized (i.e., self-sustaining) populations of 390 alien plant species from flora surveys conducted from 1986 to 2009. The occurrence records do not include artificially cultivated populations, i.e., all the data reference wild populations established outside of cultivation. We assumed that all the observed populations were present during the survey period, and the total number of grid cells in which each species was observed represented its current distribution extent. We may have underestimated the distribution extent of species since we treated species as not being distributed in a grid cell when the occurrence of the species was not recorded. However, because our focus was on quantifying the relative differences in the distribution extent among species, the possibility of underestimation should not affect our results. Among 112 herbaceous species that arrived in Hokkaido during the Meiji era, we obtained distribution data for 63 species belonging to 11 families and used these species for further analyses (for the species list, see Table S2). For each species, we calculated the total number of grid cells in which the species was observed to obtain its distribution extent across Hokkaido (hereafter, the total distribution extent). We also counted the number of occurrence grid cells that included protected areas in national, quasi-national, and prefectural nature parks (hereafter, the distribution extent in and around protected areas; Fig. 1c).

Biological and human-associated factors

For each of the 63 study species, we identified the following biological and human-associated factors that could explain the distribution extent (Table 1; for the complete dataset, see Table S2).

Species biological traits

Seven biological traits of species that are known to be associated with invasiveness were selected: seed mass, dispersal mode, maximum plant height, capability of vegetative reproduction, flowering start time and period, and life span (Pyšek and Richardson 2007; Gravuer *et al*. 2008). We collected information on these traits for each species from the published literature (Osada 1976, 2002; Satake *et al*. 1982; Shimizu *et al*. 2001; Nakayama *et al.* 2001; Shimizu 2003; Asai 2014; Tamme *et al*. 2014) and publicly available online databases (Kew Seed Information Database: http://plants.usda.gov/ Accessed 1 Feb 2017; Online Atlas of the British and Irish Flora: https://www.brc.ac.uk/Plantatlas/ Accessed 1 Feb 2017).

Introduction purpose

We identified species that were intentionally introduced for pastoral purposes based on information from Morita (1981), Nishimura (1988), and Igarashi (2001). A few species that were intentionally introduced for other purposes and species that had accidentally arrived were categorized as "others".

Cultivation frequency in pastures

All 63 alien species were assigned to one of three cultivation levels based on the frequency of seed-sowing in pastures: species that have been intentionally sown for commercial cultivation belonged to Level 3; species that have not been sown intentionally for commercial cultivation but could have been sown accidentally by becoming pasture seed contaminants belonged to Level 2; and species that have not been sown intentionally or accidentally belonged to Level 1. Two government bulletins—the lists of recommended pasture species in Hokkaido from 1914 to 2009 and the seed demand statistics of pasture plants in Hokkaido summarized by the Ministry of Agriculture, Forestry and Fisheries of Japan from 1981 to 2000 (data were not available before 1980 or after 2000)—were used to identify the intentionally sown species. Species that had contaminated pasture seeds imported into Hokkaido were drawn from the lists of pasture seed contaminants in two publications, Japan Forage Crop Seeds Association (1972) and Murayama *et al*. (1989).

The lists of pasture seed contaminants that we obtained only covered the 1970s and 1980s, but this period was considered to be the most important for the establishment and spread of pasture-related alien species in natural habitats because intensive pasture development in Hokkaido occurred during the 1970s and 1980s. According to the number of contaminated seeds per unit amount of pasture seeds described in Murayama *et al*. (1989), the contamination rate was considered to be less than 1% for all species, suggesting that contaminants had much weaker association with agriculture compared to intentionally sown species. The species that were not listed in any of the above-described references were assumed to be unsown species in pastures with no association with agriculture.

Statistical analyses

All statistical analyses were performed using the R Environment for Statistical Computing, version 3.3.1 (R Core Team 2016). We employed an information-theoretic approach to assess the relative importance of seven biological traits and two human-associated factors in explaining the distribution extent of alien species (Burnham and Anderson 2002).

Generalized linear mixed-effects models (GLMM) with a negative binomial error distribution and a log-link function were used for our analyses because of their effectiveness in analyzing non-normal and overdispersed count data (Crawley 2005; Faraway 2006). We first constructed a GLMM including the total number of occurrence grid cells (the total distribution extent) as the response variable and seven biological and two human-associated factors as explanatory variables as a global model, using the *lme4* package in R. To account for phylogenetic relatedness, we incorporated family as a random intercept in the model. We did not include interaction terms in the global model because our focus was on evaluating the importance of individual variables. All explanatory variables in the global model were tested for multicollinearity by calculating variance inflation factors (VIFs) (Dormann *et al*. 2013). The VIFs for all variables were much lower than 10, the general threshold value for detecting collinearity problems, so there was no evidence of multicollinearity among the variables (Table 2). We then generated a set of models that included all possible combinations of explanatory variables incorporated in the global model and calculated the Akaike information criterion adjusted for small sample sizes (AICc) and the Akaike weight for each model using the *MuMIn* package. Likelihood-ratio-based R^2 values for each model were also calculated to evaluate the goodness of fit. The relative importance value of each variable was obtained by summing the Akaike weights across all models in which the variable occurred (Burnham and Anderson 2002). The relative importance ranges from 0 to 1, with values closer to 1 indicating greater importance. The direction of the effects (i.e., negative or positive) of variables with high importance was determined based on the coefficients of the best model with the lowest AICc that included the variables. In addition to calculating the relative importance value of each variable, we assessed which of a set of biological or human-associated factors would be more effective in describing the total distribution extent by comparing the AICc of a model containing seven biological variables alone (hereafter, the biological model) and that of a model containing two human-associated variables alone (hereafter, the human-association model). In addition to the total distribution extent, we evaluated the importance of biological and human-associated factors in explaining the distribution extent in and around protected areas by constructing another global model that included the number of occurrence grid cells that included protected areas as the response variable.

Results

The total distribution extent across the entire prefecture greatly differed among species, i.e., it ranged from a minimum of 2 grid cells (*Trifolium incarnatum* L.) to a maximum of 1284 grid cells (*Dactylis glomerata* L.) with a median of 178 grid cells. The number of grid cells that included protected areas was 0 for several species, such as *Poa compressa* L. and *Amaranthus retroflexus* L. The maximum value, 134, was observed for *T. repens* L., and the median value was 11.

To explain the total distribution extent, the relative importance of cultivation frequency was highest among all the variables with the value of 1.0, but seed mass showed comparable importance, 0.99 (Table 2). Maximum height and flowering period were also of high importance at 0.90 and 0.86, respectively. The AICc of the human-association model and the biological model were almost the same (AICc = 845.4 and 845.8 for the former and latter, respectively). The coefficients of the best model showed that the total distribution extent across the prefecture was positively correlated with cultivation frequency, maximum height, flowering period, and the ability to reproduce vegetatively but negatively correlated with seed mass (Table 2; Fig. 2a).

For explaining the distribution extent in and around protected areas, the relative importance of cultivation frequency again showed the highest value of 1.0 followed by seed mass, for which the relative importance was 0.94; no other variables exceeded an importance value of 0.7 (Table 2). In contrast to the total distribution extent, the human-association model was clearly more effective (AICc = 531.1) than the biological model (AICc = 541.1) in describing the distribution extent in and around protected areas. The best model demonstrated that the distribution extent in and around protected areas was positively correlated with cultivation level, flowering period, and the ability to reproduce vegetatively but negatively correlated with seed mass (Table 2; Fig. 2b).

Discussion

Roles of biological traits and human association in alien plant invasions

Many previous studies have emphasized the influences of both biological and human-associated factors on plant invasion success (Thuiller *et al*. 2006; Dehnen-Schmutz *et al*. 2007; Gravuer *et al*. 2008; Maurel *et al*. 2016), but the extent to which each factor contributes has remained unclear, particularly for invasions into protected areas of high conservation priority. In the present study, we found that the relative importance of biological and human-associated factors was comparable in explaining the total distribution extent of alien plants, suggesting that species biological traits and human association almost equally contributed to invasion success across the entire study region. In contrast, when focusing on invasion in protected areas, human association was more important than biological traits, as indicated by the higher importance of cultivation frequency relative to most biological traits as well as the better predictive power of the human-association model compared to the biological model.

Because many alien species require anthropogenic disturbances to establish (Rejmánek *et al*. 2005; Colautti *et al*. 2006), natural vegetation in protected areas subjected to no or only minor disturbances is generally resistant to biological invasion, resulting in fewer occurrences of alien species in these areas compared to the surroundings (Rose and Hermanutz 2004; Pauchard *et al*. 2013). In Hokkaido, 85% of the protected areas consist of natural vegetation, and these environments are likely to be unsuitable for invaders. Nevertheless, we found a clear correlation between cultivation frequency and the distribution extent in and around protected areas, and species that were frequently cultivated in pastures were widely distributed in such areas. In Hokkaido, many nature reserves are adjacent to pastures, allowing direct seed flow to occur (Egawa 2017), and the number of reserve visitors—a major vector for dispersing the seeds of alien species into protected areas (Lonsdale 1999)—is very high (ca. 40 million people / year, Ministry of the Environment of Japan: http://www.env.go.jp/park/doc/data.html Accessed 20 April 2018).

Therefore, species that are frequently cultivated in pastures would have numerous opportunities to disperse their seeds into protected areas, and this propagule supply associated with cultivation would have played a vital role in such invasions. Furthermore, we found that introduction purpose was not correlated with invasion success in protected areas as well as in the entire region. These findings suggest that successful invasion into protected areas would be determined by a long-term human association after introduction. Although the best model showed that three out of seven examined species traits were correlated with the distribution extent in and around protected areas, the importance of most traits was moderate or relatively low, except for seed mass. The species traits that are known to be related to invasiveness, such as a high maximum height, early flowering, long reproductive period, and ability to vegetatively reproduce, are common in ruderals or competitors, which often become successful invaders in new locations (Balogh *et al*. 2003). Rose and Hermanutz (2004) predicted that the strategies of ruderal/competitor plants can be inefficient for establishment in undisturbed natural habitats, which are relatively resource-limited, because these strategies are generally resource intensive. Our results are consistent with their prediction, suggesting that species traits associated with ruderal/competitor plants, which are generally considered to be invasive, may not always be effective for establishment and/or spread in natural vegetation subjected to minor disturbances in protected areas. Among the examined species traits, seed mass was of high importance at 0.94 and exhibited a clear negative correlation with the distribution extent in and around protected areas. Small seeds can easily adhere to the body of transporters and can be dispersed widely (Fenner and Thompson 2005; Cousens *et al*. 2008), even if they are not specially adapted for dispersal vectors (Quick and Houseman 2017). These advantages of small-seeded species may have played a considerable role in the colonization of and/or spread into protected areas.

We found that species biological traits and human association contributed almost equally to invasion success across the entire prefecture, as both the biological and human-association models indicated almost equal effectiveness in describing the total distribution extent. Similarly, the relative importance value of seed mass was comparable to that of cultivation frequency, and two other species traits, maximum height and flowering period, were also of high importance. High maximum height and long flowering season are noted to be adaptive in nutrient-rich, disturbed habitats (Grime 1977). In Hokkaido, human-disturbed vegetation, such as urban areas, accounted for ca. 50% of the land. Therefore, high plant height and long reproductive phenology would have substantially contributed to invasion into such human-disturbed areas in the prefecture.

In conclusion, this study demonstrated that the relative contribution of biological and human-associated factors to invasion success can differ between the entire-area scale and the protected-area scale. We highlight that alien plant invasions into protected areas with high conservation priority would be more attributable to human association than to species-inherent biological traits.

Implications for the prevention of further invasions into protected areas

Preventing further invasions of alien plants into protected areas is a pressing matter in conserving native biodiversity (Foxcroft *et al*. 2013). Our finding regarding the great importance of cultivation frequency in explaining the distribution extent in protected areas suggests that reducing the propagule pressure associated with the commercial cultivation of alien species can be key to preventing future invasions into protected areas. For example, seed dispersal from cultivated settings needs to be minimized through effective management, such as the establishment of sufficient marginal distances between cultivated and surrounding areas. In addition, in the case of agriculture, it may be necessary to manage abandoned farmland because it can act as a vigorous source of propagules of alien plants (Pándi et al. 2014).

Another implication of our study is that attention should be paid when predicting the invasiveness of alien species from biological traits in protected areas because the traits that are generally useful for such predictions are not always valid when focusing on protected areas. For example, maximum plant height was an important predictor of invasion success across the entire prefecture (relative importance = 0.90) in our study, but this was not the case in protected areas (relative importance = 0.41). Conversely, some species traits might contribute to invasions into protected areas but not over entire areas. Future studies exploring species traits that can be associated with invasiveness in natural vegetation subjected to minor disturbances would provide useful information to effectively screen for potential invaders in protected areas.

Funding

This work was supported by the first author's institution, National Agriculture and Food Research Organization [1E16N104L1G00].

Acknowledgments

We thank the Biodiversity Division of the Hokkaido government and the Feed Division of the Ministry of Agriculture, Forestry and Fisheries of Japan for the permission to use their data, K. Hirano and K. Sanada for their advice in collecting information on seed demand statistics, N. Iwasaki for his support in GIS analysis, and A. Tomioka for her assistance in compiling information on species traits.

References

Akasaka M, Takada M, Kitagawa R, et al. (2012) Invasive non-native species attributes and invasion extent: examining the importance of grain size. *J Veg Sci* **23**:33–40.

Asai M (2014) *Weeds of Japan in Colors*. Tokyo, Japan: Zenkoku Nouson Kyouiku Kyoukai (in Japanese).

Balogh L, Botta-Dukát Z, Dancza I (2003) What kind of plants are invasive in Hungary? In Child LE, Brock JH, Brundu G, et al. (eds). *Plant Invasions: Ecological Treats and Management Solutions*. Leiden, The Netherlands: Backhuys Publishers, 131–146.

Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference*. Heidelberg, Germany: Springer.

Crawley MJ (2005) *Statistics: An Introduction Using R*. Chichester, UK: John Wiley and Sons.

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model for biological invasions. *Biol Invasions* **8**:1023–1037.

Cousens R, Dytham C, Law R (2008) *Dispersal in Plants: A Population Perspective*. Oxford, UK: Oxford University Press.

Dehnen-Schmutz K, Touza J, Perrings C, et al. (2007) The horticultural trade and ornamental plant invasions in Britain. *Conserv Biol* **21**:224–231.

Dormann CF, Elith J, Bacher S, et al. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**:27–46.

Driscoll DA, Catford JA, Barney JN, et al. (2014) New pasture plants intensify invasive species risk. *Proc Natl Acad Sci USA* **111**:16622–16627.

Drenovsky RE, Grewell BJ, Dantonio CM, et al. (2012) A functional trait perspective on plant invasion. *Ann Bot* **110**:141–153.

Egawa C (2017) Wind dispersal of alien plant species into remnant natural vegetation from adjacent agricultural fields. *Glob Ecol Conserv* **11**:33–41.

Faraway JJ (2006) *Extending the Linear Model with R: Generalized Linear, Mixed Effects and Nonparametric Regression Models*. Boca Raton, FL: Chapman and Hall.

Fenner M, Thompson K (2005) *The Ecology of Seeds*, Cambridge, UK: Cambridge University Press.

Foxcroft LC, Pyšek P, Richardson DM, et al. (2013) *Plant Invasions in Protected Areas*. Heidelberg, Germany: Springer.

Gravuer K, Sullivan JJ, Williams PA, et al. (2008) Strong human association with plant invasion success for *Trifolium* introductions to New Zealand. *Proc Natl Acad Sci USA* **105**:6344–6349.

Groves RH, Panetta FD, Virtue JG (2001) *Weed Risk Assessment*. Collingwood, Australia: CSIRO Publishing.

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* **111**:1169–1194.

Hokkaido Agricultural Experiment Station (1973) *Trends and Current Status of Grassland Statistics in Hokkaido*. Sapporo, Japan: Hokkaido Agricultural Experiment Station (in Japanese).

Hokkaido Regional Development Bureau (1967) *Report of the Comprehensive Research in Sarobetsu Region: Actual Situation at the Beginning of Sarobetsu Region Development*. Sapporo, Japan: Hokkaido Regional Development Bureau (in Japanese).

Igarashi H (2001) *The Handbook of Naturalized Plants in Hokkaido*. Sapporo, Japan: Hokkaido Research Institute for Wild Plants (in Japanese).

Japan Forage Crop Seeds Association (1972) *Research Data of Forage Crop Seeds, Vol. 3*. Tokyo, Japan: Japan Forage Crop Seeds Association (in Japanese).

459 Japan Livestock Industry Association (1976) *History of Grasslands and Forages in Japan*. Tokyo, Japan: Japan Livestock Industry Association (in Japanese).

461 Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends Ecol Evol* **20**:223–228.

463 Lonsdale WM (1994) Inviting trouble: introduced pasture species in northern Australia. *Aust J Ecol* **19**:345–354.

465 Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* **80**:1522–1536.

467 Matsushita B, Xu M, Chen J, et al. (2004) Estimation of regional net primary productivity (NPP) using a process-based ecosystem model: how important is the accuracy of climate data? *Ecol Modell* **178**:371–388.

470 Maurel N, Hanspach J, Kühn I, et al. (2016) Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. *Glob Ecol Biogeogr* **25**:1500–1509.

473 Meiners SJ, Pickett STA (2013) Plant invasions in protected landscapes: exception or expectation? In Foxcroft LC, Pyšek P, Richardson DM, et al. (eds). *Plant Invasions in Protected Areas*. Heidelberg, Germany: Springer, 43–60.

476 Morita H (1981) An outline of alien weeds in Hokkaido and some problems on their control. *J Weed Sci Tec* **26**:8–22.

478 Murayama S, Sekijo T, Tejima K, et al. (1989) Mixed foreign seeds in the import grasses seeds, part 2: discussion of family and species of mixed weed seeds in the import grasses seeds. *Journal of Hokkaido Society of Grassland Science* **23**:65–74.

481 Nakayama S, Inokuchi M, Minamitani T (2001) *Seeds of Wild Plants in Japan*. Sendai, Japan: Tohoku University Press (in Japanese).

483 Nishimura N (1988) Introduction of pasture plants and formation of plant communities in

pastures. In Yano N (ed). *Vegetation in Japan: Ecology of Invasions and Disturbances*. Tokyo, Japan: Tokai University Press, 30–39 (in Japanese).

Osada T (1976) *Colored Illustrations of Naturalized Plants of Japan*. Osaka, Japan: Hoikusha Publishing (in Japanese).

Osada T (2002) *Illustrated Grasses of Japan*. Tokyo, Japan: Heibonsha Publishers (in Japanese).

Overholt WA, Franck AR (2017) The invasive legacy of forage grass introductions into Florida. *Nat Area J* **37**:254–264.

Pándi I, Penksza K, Botta-Dukát Z, et al. (2014) People move but cultivated plants stay: abandoned farmsteads support the persistence and spread of alien plants. *Biodivers Conserv* **23**:1289–1302.

Pauchard A, Fuentes N, Jiménez A, et al. (2013) Alien plants homogenise protected areas: evidence from the landscape and regional scales in south central Chile. In Foxcroft LC, Pyšek P, Richardson DM, et al. (eds). *Plant Invasions in Protected Areas*. Heidelberg, Germany: Springer, 191–208.

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? In Nentwig W (ed). *Biological Invasions*. Heidelberg, Germany: Springer, 97–125.

Pyšek P, Jarošík V, Pergl J (2011) Alien plants introduced by different pathways differ in invasion success: unintentional introductions as a threat to natural areas. *PLoS ONE* **6**:e24890, doi:10.1371/journal.pone.0024890.

Quick ZI, Houseman GR (2017) Assessing wind and mammals as seed dispersal vectors in an invasive legume. *Weed Res* **57**: 35–43.

R core team (2016) *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.r-project.org/.

509 Rejmánek A, Richardson DM, Higgins SI, et al. (2005) Ecology of invasive plants: state of the art. In Mooney H, Mack RN, McNeely JA, et al. (eds). *Invasive Alien Species: A New Synthesis*. Washinton DC: Island Press, 104–161.

512 Rose M, Hermanutz L (2004) Are boreal ecosystems susceptible to alien plant invasion? Evidence from protected areas. *Oecologia* **139**:467–477.

514 Satake Y, Ohi J, Kitamura S, et al. (1982) *Wild Flowers of Japan, Herbaceous Plants I, П, Ш*. Tokyo, Japan: Heibonsha Publishers (in Japanese).

516 Seebens H, Blackburn TM, Dyer E, et al. (2017) No saturation in the accumulation of alien species worldwide. *Nat Commun* **8**:14435.

518 Shimizu N, Morita H, Hirota S (2001) *Pictures of Japanese Alien Plants: 600 Plant Invaders*, Tokyo, Japan: Zenkoku Nouson Kyouiku Kyoukai (in Japanese).

520 Shimizu T (2003) *Naturalized Plants of Japan*. Tokyo, Japan: Heibonsha Publishers (in Japanese).

522 Shimono Y, Konuma A (2008) Effects of human-mediated processes on weed species composition in internationally traded grain commodities. *Weed Res* **48**:10–18.

524 Simberloff D (2009) The role of propagule pressure in biological invasions. *Annu Rev Ecol Evol Syst* **40**:81–102.

526 Tamme R, Götzenberger L, Zobel M, et al. (2014) Predicting species' maximum dispersal distances from simple plant traits. *Ecology* **95**: 505–513.

528 Tateishi T (1985) Sand dunes on the coast of the sea of Okhotsk studied from the viewpoint of land reclamation. *Proceedings of the Institute of Natural Sciences, Nihon University* **20**:11–32.

531 Thuiller W, Richardson DM, Rouget M, et al. (2006) Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology* **87**:1755–1769.

Wilson JRU, Richardson DM, Rouget M, et al. (2007) Residence time and potential range: crucial considerations in modelling plant invasion. *Divers Distrib* **13**:11–12.

536 **Table 1:** Summary of the variables examined in this study. Median, maximum, and
537 minimum values are shown for continuous variables, and the levels are shown with the
538 number of included species in parentheses for categorical variables.

Explanatory variables	Variable type	Median values (max, min) or levels (number of species)
Human-associated factors		
Introduction purpose	Categorical	Pastoral use (24), others (39)
Cultivation frequency	Categorical	Level 1: Not sown (24), Level 2: Accidentally sown as a contaminant (26), Level 3: Intentionally sown for cultivation (13)
Biological factors		
Seed mass (mg)	Continuous	0.6 (10.9, 0.01)
Dispersal mode	Categorical	Unspecialized (53), animal (2), wind (8)
Maximum height (cm)	Continuous	80 (300, 15)
Vegetative reproduction	Categorical	Capable (30), not capable or unknown (33)
Flowering start month	Continuous	5 (8, 3)
Flowering period (months)	Continuous	2 (9, 1)
Life span	Categorical	Annual or biennial (28), perennial (35)

539

Table 2: Variance inflation factors (VIFs) and the relative importance (w_i) of each variable included in the global models, and the coefficients and SE of the best model with the lowest AICc. The relative importance was calculated by summing the Akaike weights across all models in which the variable occurs (N = 256).

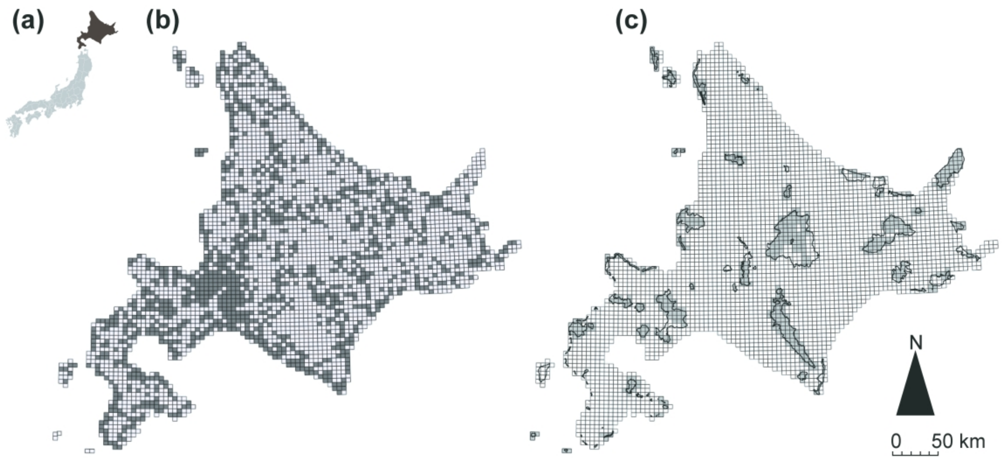
	Response: Total distribution extent				Response: Distribution extent in and around protected areas			
	VIF	w_i	Best model AICc: 824.1 R^2: 0.75 Akaike weight: 0.111		VIF	w_i	Best model AICc: 516.9 R^2: 0.75 Akaike weight: 0.076	
Variables			Coefficient	SE			Coefficient	SE
(Intercept)			3.946	0.412			1.575	0.514
Human-associated factors								
Introduction for pastoral use	1.40	0.26	-		1.31	0.26	-	
Cultivation frequency		1.00				1.00		
- Level 2	2.29		0.193	0.343	2.63		0.152	0.427
- Level 3	1.77		1.501	0.399	2.02		1.763	0.493
Biological factors								
Seed mass	1.68	0.99	-0.257	0.076	1.58	0.94	-0.228	0.100
Dispersal mode		0.39	-			0.29	-	
- Animal	1.13				1.14			
- Wind	1.73				1.83			
Maximum height	1.25	0.90	0.005	0.003	1.35	0.41	-	
Capable of vegetative reproduction	3.12	0.52	0.604	0.316	3.02	0.59	0.836	0.392
Flowering start month	2.37	0.23	-		2.51	0.29	-	
Flowering period	2.79	0.86	0.219	0.097	3.04	0.67	0.208	0.114
Perennial	3.19	0.25	-		2.99	0.26	-	

- Not included in the model.

Figure legends

Figure 1: (a) Geographic location of the study site, Hokkaido. (b) The distribution map of an example species based on occurrence records in the Hokkaido Blue List alien species database. Black-colored grid cells are those in which the species were observed. (c) Distribution of protected areas in six national, five quasi-national, and 12 prefectural-nature parks. Black solid lines indicate the areas of the parks, and gray-colored grid cells are those including protected areas in each park.

Figure 2: Relationships between (a) the total distribution extent and (b) the distribution extent in and around protected areas and nine studied variables.


(a)
(b)
(c)
N
0
50 km

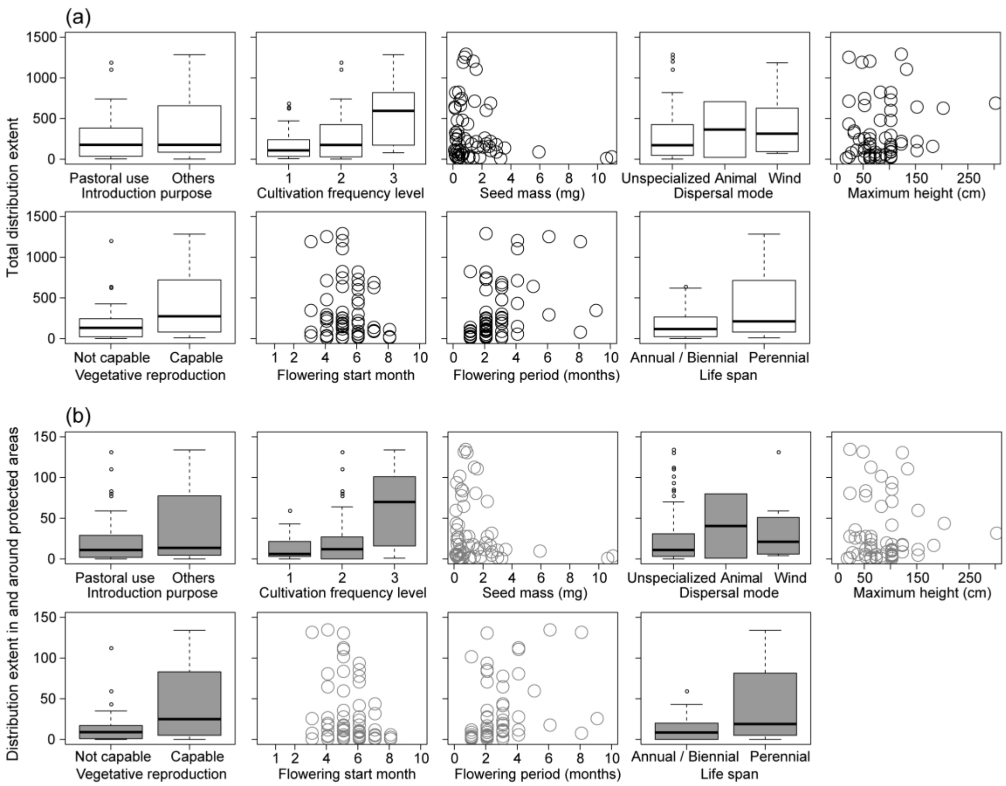

(a)
Total distribution extent
Pastoral use
Others
Introduction purpose
Cultivation frequency level
Seed mass (mg)
Unspecialized
Animal
Wind
Dispersal mode
Maximum height (cm)
Not capable
Capable
Vegetative reproduction
Flowering start month
Flowering period (months)
Annual / Biennial
Perennial
Life span
(b)
Distribution extent in and around protected areas
Pastoral use
Others
Introduction purpose
Cultivation frequency level
Seed mass (mg)
Unspecialized
Animal
Wind
Dispersal mode
Maximum height (cm)
Not capable
Capable
Vegetative reproduction
Flowering start month
Flowering period (months)
Annual / Biennial
Perennial
Life span

Table S1: The proportion of human-disturbed and natural vegetation across the entire area and in protected areas in Hokkaido. Calculation of area and percentage was done by the authors based on the vegetation map of 1/50,000 scale as of 1999 created by the Ministry of the Environment of Japan based on periodic vegetation surveys (the associated GIS data are available at: http://gis.biodic.go.jp/webgis/sc-025.html?kind=vg).

	Entire area		Protected areas	
	Area (ha)	Proportion (%)	Area (ha)	Proportion (%)
Human-disturbed vegetation				
Urban area	103,035.3	1.2	84.3	0.0
Agricultural land	1,610,766.0	19.3	410.7	0.1
Secondary grassland	394,916.9	4.7	4,566.5	1.5
Secondary forest	465,396.9	5.6	2,380.6	0.8
Planted forest	1,346,306.0	16.1	1,220.4	0.4
Subtotal	**3,920,421.0**	**46.9**	**8,662.5**	**2.8**
Natural vegetation				
Forest	3,608,403.0	43.2	213,416.3	70.7
Wet and dry grassland	177,225.0	2.1	4,279.4	14.0
Subtotal	**3,785,628.0**	**45.3**	**217,695.7**	**84.7**
Others (including open water areas)	638,950.5	7.8	37,483.6	12.4
Total	**8,345,000**	**100**	**301,962.3**	**100**

Table S2: Dataset of 63 species used in this study.

Family	Scientific name	Common name	Human association		Biological traits								Distribution extent	
			Introduction purpose [a]	Cultivation frequency Level [b]	Seed mass (mg) [c]	Dispersal mode [d]	Max height (cm) [e]	Vegetative reproduction [f]	Flowering start month [g]	Flowering end month [h]	Flowering period (months)	Life span [i]	Total	Protected areas
Poaceae	*Agrostis canina* L.	Velvety bentgrass	P	1	0.06	U	80	Y	5	6	1	P	47	3
	Agrostis gigantea Roth	Redtop	P	3	0.08	U	100	Y	6	8	2	P	813	93
	Agrostis stolonifera L.	Creeping bentgrass	P	1	0.07	U	50	Y	7	8	1	P	92	5
	Alopecurus pratensis L.	Meadow foxtail	P	2	0.9	U	120	Y	5	7	2	P	212	16
	Anthoxanthum odoratum L.	Sweet vernalgrass	P	2	0.6	U	80	Y	4	7	3	P	473	64
	Bromus inermis Leyss.	Smooth bromegrass	P	3	2.9	U	70	Y	7	8	1	P	81	1
	Bromus secalinus L.	Rye brome	O	2	10.5	U	80	N	5	8	3	A	3	0
	Dactylis glomerata L.	Orchardgrass	P	3	0.8	U	120	Y	5	7	2	P	1284	130
	Elytrigia repens (L.) Desv. ex B.D.Jackson	Quackgrass	O	2	2.1	U	90	Y	4	7	3	P	254	19
	Festuca arundinacea Schreb.	Tall fescue	P	3	2.4	U	180	Y	5	7	2	P	152	16
	Festuca pratensis Huds.	Meadow fescue	P	3	2.2	U	100	Y	6	8	2	P	594	70
	Holcus lanatus L.	Velvet grass	P	2	0.3	U	90	Y	6	7	1	P	53	8
	Lolium multiflorum Lam.	Italian ryegrass	P	3	2.9	U	100	N	5	7	2	A	173	10
	Lolium perenne L.	Perennial ryegrasses	P	3	2.2	U	60	Y	5	7	2	P	183	27
	Phleum pratense L.	Timothy	P	3	0.4	U	100	Y	6	8	2	P	722	85
	Poa compressa L.	Canadian bluegrass	P	1	0.2	U	60	Y	6	8	2	P	9	0
	Poa palustris L.	Fowl bluegrass	P	1	0.2	U	100	Y	5	7	2	P	114	5
	Poa pratensis L.	Kentucky bluegrass	P	3	0.3	U	80	Y	5	6	1	P	818	101
	Poa trivialis L.	Rough bluegrass	P	2	0.1	U	100	Y	4	6	2	P	30	3
Fabaceae	*Medicago lupulina* L.	Black medick	O	2	1.6	U	60	N	5	7	2	A	141	13
	Medicago sativa L.	Alfalfa	P	3	2.0	U	100	N	5	9	4	P	143	11
	Melilotus officinalis (L.) Pall. subsp. *albus* (Medik.) H.Ohashi et Tateishi	White sweetclover	P	1	2.5	U	120	N	6	8	2	A	213	8
	Melilotus officinalis (L.) Pall. subsp. *suaveolens* (Ledeb.) H.Ohashi	Yellow Sweetclover	P	2	2.5	U	150	N	4	6	2	A	101	4
	Trifolium hybridum L.	Alsike clover	P	3	0.7	U	50	N	5	7	2	P	248	27
	Trifolium incarnatum L.	Crimson clover	P	2	3.2	U	60	N	4	7	3	A	2	0
	Trifolium pratense L.	Red clover	P	3	1.3	U	60	N	5	9	4	P	1198	112
	Trifolium repens L.	White clover	P	3	0.7	U	20	Y	4	10	6	P	1247	134
Rosaceae	*Fragaria vesca* L.	Wild strawberry	O	1	0.3	A	20	Y	6	7	1	P	23	1
	Potentilla norvegica L.	Norwegian cinquefoil	O	2	0.1	U	60	Y	6	9	3	A	294	23
Brassicaceae	*Camelina alyssum* (Mill.) Thell.		O	2	0.3	U	70	N	5	6	1	A	3	0
	Lepidium virginicum L.	Virginia pepperweed	O	2	0.5	U	60	N	5	7	2	A	47	0
	Sisymbrium officinale (L.) Scop.	Hedgemustard	O	2	0.3	U	80	N	4	6	2	A	22	0
	Thlaspi arvense L.	Field pennycress	O	2	1.0	U	60	N	3	5	2	A	27	0
Polygonaceae	*Fallopia convolvulus* (L.) Á.Löve		O	2	5.8	U	100	N	6	9	3	A	83	9
	Polygonum aviculare L. subsp. *depressum* (Meisn.) Arcang.		O	2	0.9	U	20	N	6	10	4	A	426	27
	Rumex acetosella L. subsp. *pyrenaicus* (Pourret ex Lapeyr.) Akeroyd		O	2	0.5	U	50	Y	5	7	2	P	740	83
	Rumex crispus L.	Curly dock	O	2	1.5	U	150	Y	4	7	3	P	210	11
	Rumex obtusifolius L.	Bitter dock	O	2	1.5	U	130	Y	5	9	4	P	1099	110
Caryophyllaceae	*Silene armeria* L.	Sweet William silene	O	1	0.1	U	60	N	5	8	3	A	244	17
	Silene noctiflora L.	Nightflowering silene	O	2	1.0	U	60	N	5	6	1	A	11	1
	Silene vulgaris (Moench) Garcke	Maidenstears	O	1	1.3	U	50	N	6	8	2	P	12	2
	Spergula arvensis L. var. *arvensis*		O	1	0.3	U	60	N	6	9	3	A	178	10
Amaranthaceae	*Amaranthus albus* L.	Prostrate pigweed	O	1	0.3	U	15	N	8	10	2	A	7	0
	Amaranthus blitum L.	Purple amaranth	O	1	0.6	U	70	N	6	10	4	A	49	5
	Amaranthus retroflexus L.	Redroot pigweed	O	2	0.4	U	100	N	7	9	2	A	88	0
	Chenopodium hybridum L.	Mapleleaf goosefoot	O	1	1.8	U	100	N	8	9	1	A	17	2
Phytolaccaceae	*Phytolacca acinosa* Roxb.		O	1	10.9	U	100	N	6	9	3	P	23	3
Plantaginaceae	*Linaria vulgaris* Mill.	Butter and eggs	O	1	0.2	W	100	Y	7	9	2	P	81	4
	Plantago lanceolata L.	Narrowleaf plantain	O	2	1.4	A	20	Y	4	8	4	P	707	80
	Veronica arvensis L.	Corn speedwell	O	1	0.1	U	40	N	4	6	2	A	237	26
Lamiaceae	*Galeopsis bifida* Boenn.	Splitlip hempnettle	O	1	3.5	U	50	N	7	8	1	A	132	11
Asteraceae	*Achillea millefolium* L.	Common yarrow	O	1	0.2	U	100	Y	6	9	3	P	471	41
	Cichorium intybus L.	Chicory	O	1	1.2	U	120	N	6	9	3	P	181	17
	Erigeron annuus (L.) Pers.	Eastern daisy fleabane	O	1	0.03	W	150	N	5	10	5	A	635	59
	Erigeron canadensis L.	Canadian horseweed	O	1	0.05	W	200	N	7	10	3	A	621	43
	Gnaphalium uliginosum L.	Marsh cudweed	O	1	0.01	W	35	N	8	10	2	A	105	5
	Leucanthemum vulgare Lam.	Oxeye daisy	O	2	0.4	U	50	Y	6	9	3	P	654	77
	Matricaria matricarioides (Less.) Ced.Porter ex Britton		O	1	0.08	U	30	N	5	7	2	A	318	35
	Rudbeckia laciniata L.	Cutleaf coneflower	O	1	2.5	U	300	Y	7	10	3	P	682	31
	Senecio vulgaris L.	Old-man-in-the-Spring	O	2	0.2	W	30	N	3	12	9	A	340	25
	Sonchus asper (L.) Hill	Spiny sowthistle	O	2	0.3	W	100	N	4	10	6	A	287	17
	Taraxacum laevigatum (Willd.) DC.	Rock dandelion	O	1	0.6	W	25	Y	3	11	8	P	73	7
	Taraxacum officinale Weber ex F.H.Wigg.	Dandelion	O	2	0.6	W	45	Y	3	11	8	P	1185	131

[a] Introduction purpose P: pastoral use, O: others. References: Morita (1981), Nishimura (1988), Igarashi (2001).

[b] Cultivation frequency Level 1: not sown, Level 2: accidentally sown as a contaminant, Level 3: intentionally sown for commerical cultivation. References: The list of reccomended pasture species in Hokkaido from 1914 to 2009, the seed demand statistics of pasture plants in Hokkaido summarized by the Ministry of Agriculture, Forestry and Fisheries of Japan from 1981 to 2000, Japan Forage Crop Seeds Association (1972), Murayama et al. (1989).

[c] Seed mass References: Kew Seed Information Database: http://plants.usda.gov/ (Accessed 1 Feb 2017), Shimizu et al. (2001), Asai (2014).

[d] Dispersal mode U: unspecialized, A: animal (attachment or ingestion), W: wind. References: Nakayama et al. (2001), Asai (2014), Tamme et al. (2014).

[e] Max height References: Osada (1976, 2002), Satake et al. (1982), Shimizu (2003).

[f] Vegetative reproduction Y: capable, N: not capable or unknown. References: Satake et al. (1982), Osada (2002), Asai (2014), Online Atlas of the British and Irish Flora: https://www.brc.ac.uk/Plantatlas/ (Accessed 1 Feb 2017).

[g] Flowering start month References: Satake et al. (1982), Osada (2002), Shimizu (2003), Asai (2014).

[h] Flowering end month References: Satake et al. (1982), Osada (2002), Shimizu (2003), Asai (2014). Note that this parameter was not incorporated in the analysis.

[i] Life span A: annual or biennial, P: perennial. References: Osada (1976, 2002), Satake et al. (1982), Shimizu (2003).