

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

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1 Running title: Factors associated with plant invasion success

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

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## 24 **Abstract**

### 25 *Aims*

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

### 33 *Methods*

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

### 45 *Important Findings*

46 In explaining the distribution extent across the entire prefecture, species biological traits  
47 and human-associated factors showed comparable importance; cultivation frequency  
48 exhibited the highest importance value closely followed by seed mass, maximum height,

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4 49 and flowering period. In contrast, when focusing on protected areas, human association was  
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6 50 more important than biological traits, as indicated by the greatest importance of cultivation  
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8 51 frequency and much lower values for most biological traits. The results demonstrated that  
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10 52 species biological traits and human association almost equally contributed to invasion  
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13 53 success across the entire region, while invasions into protected areas were more attributable  
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15 54 to human association than to biological traits. We highlight that the control of propagule  
16  
17 55 pressure associated with artificial cultivation may be key to preventing further invasions  
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20 56 into protected areas.  
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24 58 **Keywords:** agricultural use, biological invasion, distribution, nature reserve, pasture plants  
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## 60 **Introduction**

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

81 From a conservation perspective, clarification of the mechanisms of invasion in  
82 protected areas is of particular interest because the establishment of alien species is most  
83 problematic in protected areas, where the conservation of native biodiversity is mandated  
84 (Foxcroft *et al.* 2013). Protected areas generally maintain natural vegetation with fewer

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4 85 anthropogenic disturbances, and because many alien species fail to establish without  
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6 86 artificial disturbances that increase resource availability (Rejmánek *et al.* 2005; Colautti *et*  
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8 87 *al.* 2006), the invasibility of vegetation in protected areas is potentially lower than that of  
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10 88 vegetation in surrounding areas, including those subjected to human disturbance (Rose and  
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12 89 Hermanutz 2004; Pauchard *et al.* 2013). Considering the low invasibility of the involved  
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14 90 vegetation, it is probable that the relative importance of species biological traits and human  
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16 91 association in determining invasion success in protected areas differs from the general  
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18 92 patterns covering the entire area in the region. Specifically, human association may play a  
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20 93 more important role than species biological traits in invasions into protected areas because  
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22 94 an extrinsic supply of propagules is vital for the invasion of areas with environmental  
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24 95 resistance (Simberloff 2009), whereas such a supply may not be essential for successful  
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26 96 invasion into disturbed vegetation outside protected areas. Evaluation of the relative  
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28 97 contribution of species biological traits and human association to invasion success in  
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30 98 protected areas and across entire regions, including disturbed areas, will provide essential  
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32 99 information for understanding general and protected-area-specific invasion mechanisms  
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34 100 and potentially effective management solutions for alien plants.

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40 101 Here, we quantified the relative importance of species biological traits and association  
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42 102 with human activity to the invasion success of alien plants in protected areas and across the  
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44 103 entire region of Hokkaido Prefecture, northern Japan, using distribution extent as a  
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46 104 quantitative measure of invasion success (Wilson *et al.* 2007; Pyšek *et al.* 2011; Akasaka *et*  
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48 105 *al.* 2012). As a human activity that can promote alien plant invasions, we considered  
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50 106 agriculture because it is the means by which large numbers of alien plant species are  
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52 107 introduced and distributed into novel locations (Lonsdale 1994; Driscoll *et al.* 2014;  
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54 108 Overholt and Franck 2017). In Hokkaido, grassland-based dairy farming has been very  
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56 109 common, and many pastures are adjacent to nature reserves (Egawa 2017). Therefore, we  
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4 110 expected that association with pastoral agriculture would be an important factor in  
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6 111 explaining the invasion success of alien plants in protected areas as well as the entire area  
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8 112 of the prefecture, so we incorporated two agriculture-related variables, i.e., introduction for  
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10 113 the purpose of agricultural use (representing the association at the time of introduction) and  
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12 114 cultivation frequency (representing the association after the introduction). We specifically  
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14 115 asked the following questions: What is the relative importance of biological and human-  
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16 116 associated factors in determining invasion success in protected areas and across the entire  
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18 117 prefecture, and what are the main factors that should be managed to prevent further  
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20 118 invasions into protected areas?  
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## 27 120 **Materials and methods**

### 28 29 121 **Study site**

#### 30 31 122 *Overview of Hokkaido*

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33 123 The study site, Hokkaido, is the northernmost prefecture in Japan and consists of one main  
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35 124 island and several small islands, with a total area of 8,345,000 ha (Fig. 1a). The climate in  
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37 125 Hokkaido is categorized as a temperate subarctic climate with an annual precipitation of  
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39 126 800–1500 mm and an annual mean temperature of 6–10°C (Matsushita *et al.* 2004).  
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43 127 Hokkaido Prefecture remained largely unexplored until the beginning of the land  
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45 128 development effort led by the Meiji government in 1869 (Japan Livestock Industry  
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47 129 Association 1976). Since that time, the land was gradually developed, but the area of  
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49 130 pastures was less than 65,000 ha, which was 0.8% of the whole Hokkaido area, as of 1960  
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51 131 (Hokkaido Agricultural Experiment Station 1973). Large-scale, intensive pasture  
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53 132 development in Hokkaido began in the 1960s, which dramatically increased the area of  
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55 133 pastures (Japan Livestock Industry Association 1976), although unprofitable pastures were  
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57 134 often abandoned (Hokkaido Regional Development Bureau 1967; Tateishi 1985). As of  
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4 135 2005, pastures occupied 515,900 ha, constituting 6% of the whole Hokkaido area.

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6 136 By the end of the Meiji era in 1912, more than 50 alien plant species had been  
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8 137 intentionally introduced to Hokkaido for use in pastoral agriculture (Nishimura 1988),  
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10 138 although many were recognized as unsuitable and not used for commercial cultivation  
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12 139 (Japan Livestock Industry Association 1976). Since 1914, the Hokkaido government has  
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14 140 regularly designated well-qualified species as recommended based on the results of  
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16 141 cultivation trials and has encouraged their cultivation. Most species that have been  
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18 142 commercially cultivated to date were the government-recommended species introduced  
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20 143 during the Meiji era, although the introduction of pasture plants continued after this period.  
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24 144 Hokkaido currently has six national, five quasi-national, and 12 prefectural nature  
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26 145 parks, in which several types of nature reserves have been established to conserve native  
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28 146 landscapes and biodiversity. Among all the types of nature reserves, the special protection  
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30 147 areas and the first type of the protection areas (hereafter, these two reserve types are  
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32 148 collectively called protected areas) are considered the most important territories with the  
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34 149 highest conservation priority and are protected by the strictest regulations. Protected areas  
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36 150 account for 3.6% of the total area of Hokkaido. As commonly found in various countries  
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38 151 (Meiners and Pickett 2013), nature parks in Hokkaido lie within a matrix of human-  
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40 152 disturbed land and some are directly adjacent to pastures (Egawa 2017).  
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47 154 *Vegetation across the entire area and in protected areas in Hokkaido*

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49 155 According to the vegetation map from 1999 created by the Ministry of the Environment of  
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51 156 Japan (the associated GIS data are available at [http://gis.biodic.go.jp/webgis/sc-](http://gis.biodic.go.jp/webgis/sc-025.html?kind=v&g)  
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53 157 [025.html?kind=v&g](http://gis.biodic.go.jp/webgis/sc-025.html?kind=v&g) Accessed 26 Jul 2017), the percentages of human-disturbed vegetation  
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55 158 (including urban areas, agricultural land, secondary forest and grassland, and planted  
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57 159 forest), natural vegetation (including wet and dry grasslands and forest) and other areas  
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4 160 (including open water areas) across Hokkaido are 46.9%, 45.3%, and 7.8%, respectively  
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6 161 (Table S1). Heavily disturbed areas, i.e., urban areas and agricultural land, account for  
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8 162 20.5% of the whole prefecture. On the other hand, most protected areas consist of natural  
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10 163 vegetation (84.7%), and the percentage of human-disturbed vegetation is small (2.8%).  
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12 164 Other areas including open water occupy 12.4% of the total protected areas. Most of the  
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14 165 human-disturbed vegetation in protected areas is secondary grasslands and forests, and the  
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16 166 percentage of urban areas and agricultural land is 0.1% of the total protected areas (Table  
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18 167 S1).  
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#### 25 169 **Study species and their distribution data**

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27 170 We limited our study species to those introduced (either intentionally or accidentally) to  
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29 171 Hokkaido during the same period, i.e., the Meiji era from 1869 to 1912, to eliminate the  
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31 172 effects of residence time, and we focused on identifying the influences of species biological  
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33 173 traits and human association. Candidate species were identified based on Nishimura (1988)  
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35 174 and Igarashi (2001). Only herbaceous species were considered since there were very few  
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37 175 tree species introduced during the Meiji era (Igarashi 2001). Because nearly 100 years have  
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39 176 passed since their introduction, candidate herbaceous species likely had sufficient time to  
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41 177 expand their distribution ranges in Hokkaido. The plant nomenclature was based on YList  
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43 178 (<http://ylist.info> Accessed 29 Jan 2017).  
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47 179 To estimate the distribution extent of alien species, we used occurrence records at a  
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49 180 spatial resolution of 5-km mesh grid units (the Five-Fold Mesh) in the Hokkaido Blue List  
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51 181 (BL) alien species database (<http://bluelist.ies.hro.or.jp/> Accessed 1 March 2017; Fig. 1b).  
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53 182 The occurrence records in the BL database were compiled from 44,833 observations of  
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55 183 naturalized (i.e., self-sustaining) populations of 390 alien plant species from flora surveys  
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57 184 conducted from 1986 to 2009. The occurrence records do not include artificially cultivated  
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4 185 populations, i.e., all the data reference wild populations established outside of cultivation.  
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6 186 We assumed that all the observed populations were present during the survey period, and  
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8 187 the total number of grid cells in which each species was observed represented its current  
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10 188 distribution extent. We may have underestimated the distribution extent of species since we  
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12 189 treated species as not being distributed in a grid cell when the occurrence of the species was  
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14 190 not recorded. However, because our focus was on quantifying the relative differences in the  
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16 191 distribution extent among species, the possibility of underestimation should not affect our  
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18 192 results. Among 112 herbaceous species that arrived in Hokkaido during the Meiji era, we  
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20 193 obtained distribution data for 63 species belonging to 11 families and used these species for  
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22 194 further analyses (for the species list, see Table S2). For each species, we calculated the total  
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24 195 number of grid cells in which the species was observed to obtain its distribution extent  
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26 196 across Hokkaido (hereafter, the total distribution extent). We also counted the number of  
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28 197 occurrence grid cells that included protected areas in national, quasi-national, and  
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30 198 prefectural nature parks (hereafter, the distribution extent in and around protected areas;  
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32 199 Fig. 1c).  
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#### 201 **Biological and human-associated factors**

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

##### 205 *Species biological traits*

206 Seven biological traits of species that are known to be associated with invasiveness were  
207 selected: seed mass, dispersal mode, maximum plant height, capability of vegetative  
208 reproduction, flowering start time and period, and life span (Pyšek and Richardson 2007;  
209 Gravuer *et al.* 2008). We collected information on these traits for each species from the  
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4 210 published literature (Osada 1976, 2002; Satake *et al.* 1982; Shimizu *et al.* 2001; Nakayama  
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6 211 *et al.* 2001; Shimizu 2003; Asai 2014; Tamme *et al.* 2014) and publicly available online  
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8 212 databases (Kew Seed Information Database: <http://plants.usda.gov/> Accessed 1 Feb 2017;  
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10 213 Online Atlas of the British and Irish Flora: <https://www.brc.ac.uk/Plantatlas/> Accessed 1  
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12 214 Feb 2017).

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### 17 216 *Introduction purpose*

19 217 We identified species that were intentionally introduced for pastoral purposes based on  
20 218 information from Morita (1981), Nishimura (1988), and Igarashi (2001). A few species that  
21 219 were intentionally introduced for other purposes and species that had accidentally arrived  
22 220 were categorized as “others”.

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### 31 222 *Cultivation frequency in pastures*

33 223 All 63 alien species were assigned to one of three cultivation levels based on the frequency  
34 224 of seed-sowing in pastures: species that have been intentionally sown for commercial  
35 225 cultivation belonged to Level 3; species that have not been sown intentionally for  
36 226 commercial cultivation but could have been sown accidentally by becoming pasture seed  
37 227 contaminants belonged to Level 2; and species that have not been sown intentionally or  
38 228 accidentally belonged to Level 1. Two government bulletins—the lists of recommended  
39 229 pasture species in Hokkaido from 1914 to 2009 and the seed demand statistics of pasture  
40 230 plants in Hokkaido summarized by the Ministry of Agriculture, Forestry and Fisheries of  
41 231 Japan from 1981 to 2000 (data were not available before 1980 or after 2000)—were used to  
42 232 identify the intentionally sown species. Species that had contaminated pasture seeds  
43 233 imported into Hokkaido were drawn from the lists of pasture seed contaminants in two  
44 234 publications, Japan Forage Crop Seeds Association (1972) and Murayama *et al.* (1989).

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4 235 The lists of pasture seed contaminants that we obtained only covered the 1970s and 1980s,  
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6 236 but this period was considered to be the most important for the establishment and spread of  
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8 237 pasture-related alien species in natural habitats because intensive pasture development in  
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10 238 Hokkaido occurred during the 1970s and 1980s. According to the number of contaminated  
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12 239 seeds per unit amount of pasture seeds described in Murayama *et al.* (1989), the  
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14 240 contamination rate was considered to be less than 1% for all species, suggesting that  
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16 241 contaminants had much weaker association with agriculture compared to intentionally sown  
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18 242 species. The species that were not listed in any of the above-described references were  
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20 243 assumed to be unsown species in pastures with no association with agriculture.  
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#### 245 **Statistical analyses**

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

250 Generalized linear mixed-effects models (GLMM) with a negative binomial error  
251 distribution and a log-link function were used for our analyses because of their  
252 effectiveness in analyzing non-normal and overdispersed count data (Crawley 2005;  
253 Faraway 2006). We first constructed a GLMM including the total number of occurrence  
254 grid cells (the total distribution extent) as the response variable and seven biological and  
255 two human-associated factors as explanatory variables as a global model, using the *lme4*  
256 package in R. To account for phylogenetic relatedness, we incorporated family as a random  
257 intercept in the model. We did not include interaction terms in the global model because  
258 our focus was on evaluating the importance of individual variables. All explanatory  
259 variables in the global model were tested for multicollinearity by calculating variance  
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4 260 inflation factors (VIFs) (Dormann *et al.* 2013). The VIFs for all variables were much lower  
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6 261 than 10, the general threshold value for detecting collinearity problems, so there was no  
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8 262 evidence of multicollinearity among the variables (Table 2). We then generated a set of  
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10 263 models that included all possible combinations of explanatory variables incorporated in the  
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12 264 global model and calculated the Akaike information criterion adjusted for small sample  
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14 265 sizes (AICc) and the Akaike weight for each model using the *MuMIn* package. Likelihood-  
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16 266 ratio-based  $R^2$  values for each model were also calculated to evaluate the goodness of fit.  
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18 267 The relative importance value of each variable was obtained by summing the Akaike  
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20 268 weights across all models in which the variable occurred (Burnham and Anderson 2002).  
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22 269 The relative importance ranges from 0 to 1, with values closer to 1 indicating greater  
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24 270 importance. The direction of the effects (i.e., negative or positive) of variables with high  
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26 271 importance was determined based on the coefficients of the best model with the lowest  
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28 272 AICc that included the variables. In addition to calculating the relative importance value of  
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30 273 each variable, we assessed which of a set of biological or human-associated factors would  
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32 274 be more effective in describing the total distribution extent by comparing the AICc of a  
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34 275 model containing seven biological variables alone (hereafter, the biological model) and that  
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36 276 of a model containing two human-associated variables alone (hereafter, the human-  
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38 277 association model). In addition to the total distribution extent, we evaluated the importance  
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40 278 of biological and human-associated factors in explaining the distribution extent in and  
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42 279 around protected areas by constructing another global model that included the number of  
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44 280 occurrence grid cells that included protected areas as the response variable.  
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## 54 282 **Results**

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57 283 The total distribution extent across the entire prefecture greatly differed among species, i.e.,  
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59 284 it ranged from a minimum of 2 grid cells (*Trifolium incarnatum* L.) to a maximum of 1284

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4 285 grid cells (*Dactylis glomerata* L.) with a median of 178 grid cells. The number of grid cells  
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6 286 that included protected areas was 0 for several species, such as *Poa compressa* L. and  
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8 287 *Amaranthus retroflexus* L. The maximum value, 134, was observed for *T. repens* L., and  
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10 288 the median value was 11.

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13 289 To explain the total distribution extent, the relative importance of cultivation  
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15 290 frequency was highest among all the variables with the value of 1.0, but seed mass showed  
16  
17 291 comparable importance, 0.99 (Table 2). Maximum height and flowering period were also of  
18  
19 292 high importance at 0.90 and 0.86, respectively. The AICc of the human-association model  
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21 293 and the biological model were almost the same (AICc = 845.4 and 845.8 for the former and  
22  
23 294 latter, respectively). The coefficients of the best model showed that the total distribution  
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25 295 extent across the prefecture was positively correlated with cultivation frequency, maximum  
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27 296 height, flowering period, and the ability to reproduce vegetatively but negatively correlated  
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29 297 with seed mass (Table 2; Fig. 2a).

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33 298 For explaining the distribution extent in and around protected areas, the relative  
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35 299 importance of cultivation frequency again showed the highest value of 1.0 followed by seed  
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37 300 mass, for which the relative importance was 0.94; no other variables exceeded an  
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39 301 importance value of 0.7 (Table 2). In contrast to the total distribution extent, the human-  
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41 302 association model was clearly more effective (AICc = 531.1) than the biological model  
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43 303 (AICc = 541.1) in describing the distribution extent in and around protected areas. The best  
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45 304 model demonstrated that the distribution extent in and around protected areas was  
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47 305 positively correlated with cultivation level, flowering period, and the ability to reproduce  
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49 306 vegetatively but negatively correlated with seed mass (Table 2; Fig. 2b).

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## 55 56 57 308 **Discussion**

### 58 59 309 **Roles of biological traits and human association in alien plant invasions**

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4 310 Many previous studies have emphasized the influences of both biological and human-  
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6 311 associated factors on plant invasion success (Thuiller *et al.* 2006; Dehnen-Schmutz *et al.*  
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8 312 2007; Gravuer *et al.* 2008; Maurel *et al.* 2016), but the extent to which each factor  
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10 313 contributes has remained unclear, particularly for invasions into protected areas of high  
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12 314 conservation priority. In the present study, we found that the relative importance of  
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14 315 biological and human-associated factors was comparable in explaining the total distribution  
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16 316 extent of alien plants, suggesting that species biological traits and human association almost  
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18 317 equally contributed to invasion success across the entire study region. In contrast, when  
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20 318 focusing on invasion in protected areas, human association was more important than  
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22 319 biological traits, as indicated by the higher importance of cultivation frequency relative to  
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24 320 most biological traits as well as the better predictive power of the human-association model  
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26 321 compared to the biological model.

31 322 **Because many alien species require anthropogenic disturbances to establish**  
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33 323 (Rejmánek *et al.* 2005; Colautti *et al.* 2006), natural vegetation in protected areas subjected  
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35 324 to no or only minor disturbances is generally resistant to biological invasion, resulting in  
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37 325 fewer occurrences of alien species in these areas compared to the surroundings (Rose and  
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39 326 Hermanutz 2004; Pauchard *et al.* 2013). In Hokkaido, 85% of the protected areas consist of  
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41 327 natural vegetation, and these environments are likely to be unsuitable for invaders.  
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43 328 Nevertheless, we found a clear correlation between cultivation frequency and the  
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45 329 distribution extent in and around protected areas, and species that were frequently  
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47 330 cultivated in pastures were widely distributed in such areas. In Hokkaido, many nature  
48  
49 331 reserves are adjacent to pastures, allowing direct seed flow to occur (Egawa 2017), and the  
50  
51 332 number of reserve visitors—a major vector for dispersing the seeds of alien species into  
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53 333 protected areas (Lonsdale 1999)—is very high (ca. 40 million people / year, Ministry of the  
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55 334 Environment of Japan: <http://www.env.go.jp/park/doc/data.html> Accessed 20 April 2018).



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4 335 Therefore, species that are frequently cultivated in pastures would have numerous  
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6 336 opportunities to disperse their seeds into protected areas, and this propagule supply  
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8 337 associated with cultivation would have played a vital role in such invasions. Furthermore,  
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10 338 we found that introduction purpose was not correlated with invasion success in protected  
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12 339 areas as well as in the entire region. These findings suggest that successful invasion into  
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14 340 protected areas would be determined by a long-term human association after introduction.  
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16 341 Although the best model showed that three out of seven examined species traits were  
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18 342 correlated with the distribution extent in and around protected areas, the importance of most  
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20 343 traits was moderate or relatively low, except for seed mass. The species traits that are  
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22 344 known to be related to invasiveness, such as a high maximum height, early flowering, long  
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24 345 reproductive period, and ability to vegetatively reproduce, are common in ruderals or  
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26 346 competitors, which often become successful invaders in new locations (Balogh *et al.* 2003).  
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28 347 Rose and Hermanutz (2004) predicted that the strategies of ruderal/competitor plants can be  
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30 348 inefficient for establishment in undisturbed natural habitats, which are relatively resource-  
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32 349 limited, because these strategies are generally resource intensive. Our results are consistent  
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34 350 with their prediction, suggesting that species traits associated with ruderal/competitor  
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36 351 plants, which are generally considered to be invasive, may not always be effective for  
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38 352 establishment and/or spread in natural vegetation subjected to minor disturbances in  
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40 353 protected areas. Among the examined species traits, seed mass was of high importance at  
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42 354 0.94 and exhibited a clear negative correlation with the distribution extent in and around  
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44 355 protected areas. Small seeds can easily adhere to the body of transporters and can be  
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46 356 dispersed widely (Fenner and Thompson 2005; Cousens *et al.* 2008), even if they are not  
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48 357 specially adapted for dispersal vectors (Quick and Houseman 2017). These advantages of  
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50 358 small-seeded species may have played a considerable role in the colonization of and/or  
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52 359 spread into protected areas.  
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4 360 We found that species biological traits and human association contributed almost  
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6 361 equally to invasion success across the entire prefecture, as both the biological and human-  
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8 362 association models indicated almost equal effectiveness in describing the total distribution  
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10 363 extent. Similarly, the relative importance value of seed mass was comparable to that of  
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12 364 cultivation frequency, and two other species traits, maximum height and flowering period,  
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14 365 were also of high importance. High maximum height and long flowering season are noted  
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16 366 to be adaptive in nutrient-rich, disturbed habitats (Grime 1977). In Hokkaido, human-  
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18 367 disturbed vegetation, such as urban areas, accounted for ca. 50% of the land. Therefore,  
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20 368 high plant height and long reproductive phenology would have substantially contributed to  
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22 369 invasion into such human-disturbed areas in the prefecture.

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27 370 In conclusion, this study demonstrated that the relative contribution of biological and  
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29 371 human-associated factors to invasion success can differ between the entire-area scale and  
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31 372 the protected-area scale. We highlight that alien plant invasions into protected areas with  
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33 373 high conservation priority would be more attributable to human association than to species-  
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35 374 inherent biological traits.

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#### 39 40 376 **Implications for the prevention of further invasions into protected areas**

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42 377 **Preventing further invasions of alien plants into protected areas is a pressing matter in**  
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44 378 **conserving native biodiversity** (Foxcroft *et al.* 2013). Our finding regarding the great  
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46 379 importance of cultivation frequency in explaining the distribution extent in protected areas  
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48 380 suggests that reducing the propagule pressure associated with the commercial cultivation of  
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50 381 alien species can be key to preventing future invasions into protected areas. For example,  
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52 382 seed dispersal from cultivated settings needs to be minimized through effective  
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54 383 management, such as the establishment of sufficient marginal distances between cultivated  
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56 384 and surrounding areas. In addition, in the case of agriculture, it may be necessary to manage  
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4 385 abandoned farmland because it can act as a vigorous source of propagules of alien plants  
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6 386 (Pándi et al. 2014).

8 387 Another implication of our study is that attention should be paid when predicting the  
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10 388 invasiveness of alien species from biological traits in protected areas because the traits that  
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12 389 are generally useful for such predictions are not always valid when focusing on protected  
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14 390 areas. For example, maximum plant height was an important predictor of invasion success  
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16 391 across the entire prefecture (relative importance = 0.90) in our study, but this was not the  
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18 392 case in protected areas (relative importance = 0.41). Conversely, some species traits might  
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20 393 contribute to invasions into protected areas but not over entire areas. Future studies  
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22 394 exploring species traits that can be associated with invasiveness in natural vegetation  
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24 395 subjected to minor disturbances would provide useful information to effectively screen for  
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26 396 potential invaders in protected areas.  
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55 407 compiling information on species traits.  
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For Peer Review



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),<br>Level 2: Accidentally sown as a contaminant (26),<br>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),<br>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),<br>perennial (35)   |

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

| Variables                          | Response: Total distribution extent |       |   |       | Response: Distribution extent in and around protected areas |       |   |       |
|------------------------------------|-------------------------------------|-------|---|-------|---|-------|---|-------|
|                                    | VIF                                 | $w_i$ | Best model<br>AICc: 824.1<br>$R^2$ : 0.75<br>Akaike weight: 0.111 |       | VIF   | $w_i$ | Best model<br>AICc: 516.9<br>$R^2$ : 0.75<br>Akaike weight: 0.076 |       |
|                                    |                                     |       | 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  | -   |       |

544 - Not included in the model.

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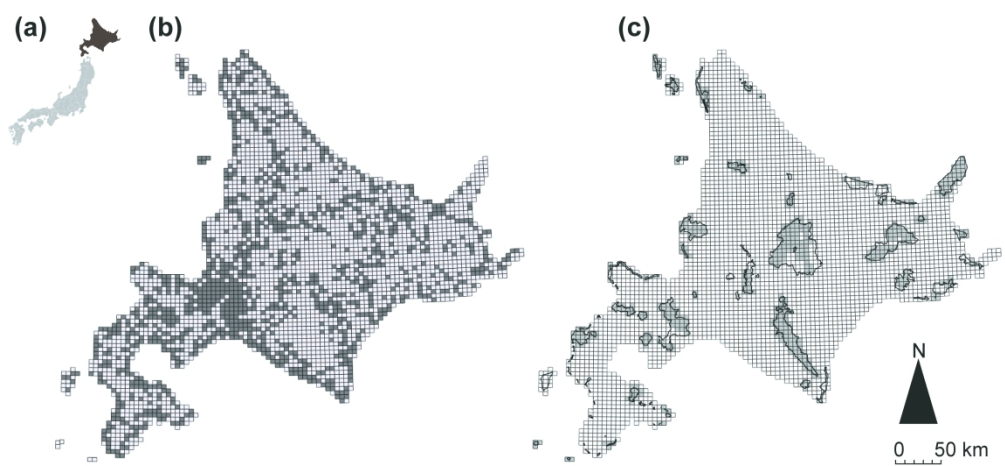
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5 546 **Figure legends**  
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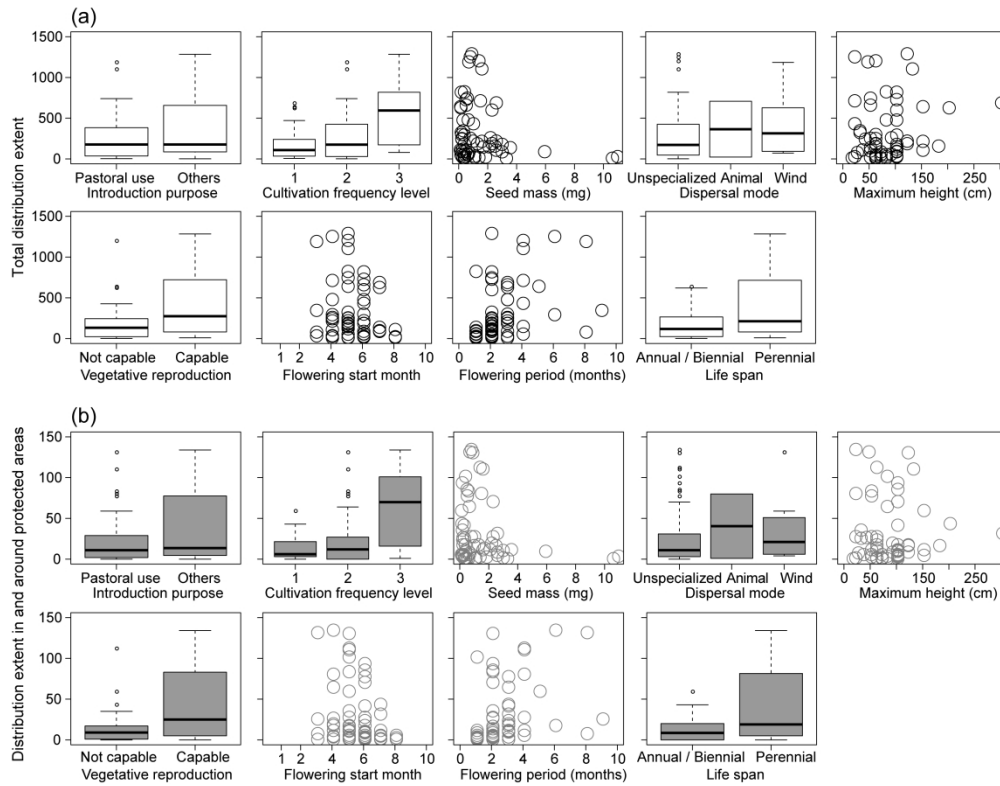
7 547 **Figure 1:** (a) Geographic location of the study site, Hokkaido. (b) The distribution map of  
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9 548 an example species based on occurrence records in the Hokkaido Blue List alien species  
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11 549 database. Black-colored grid cells are those in which the species were observed. (c)  
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13 550 Distribution of protected areas in six national, five quasi-national, and 12 prefectural-nature  
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15 551 parks. Black solid lines indicate the areas of the parks, and gray-colored grid cells are those  
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17 552 including protected areas in each park.  
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23 554 **Figure 2:** Relationships between (a) the total distribution extent and (b) the distribution  
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25 555 extent in and around protected areas and nine studied variables.  
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**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=vj>).

|                                     | Entire area        |                | Protected areas  |                |
|-------------------------------------|--------------------|----------------|------------------|----------------|
|                                     | Area (ha)          | Proportion (%) | Area (ha)        | Proportion (%) |
| <b>Human-disturbed vegetation</b>   |                    |                |                  |                |
| 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            |
| <b>Subtotal</b>                     | <b>3,920,421.0</b> | <b>46.9</b>    | <b>8,662.5</b>   | <b>2.8</b>     |
| <b>Natural vegetation</b>           |                    |                |                  |                |
| 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           |
| <b>Subtotal</b>                     | <b>3,785,628.0</b> | <b>45.3</b>    | <b>217,695.7</b> | <b>84.7</b>    |
| Others (including open water areas) | 638,950.5          | 7.8            | 37,483.6         | 12.4           |
| <b>Total</b>                        | <b>8,345,000</b>   | <b>100</b>     | <b>301,962.3</b> | <b>100</b>     |

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

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

<sup>a</sup> Introduction purpose P: pastoral use, O: others. References: Morita (1981), Nishimura (1988), Igarashi (2001).<sup>b</sup> Cultivation frequency Level 1: not sown, Level 2: accidentally sown as a contaminant, Level 3: intentionally sown for commercial cultivation. References: The list of recommended 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).<sup>c</sup> Seed mass References: Kew Seed Information Database: <http://plants.usda.gov/> (Accessed 1 Feb 2017), Shimizu et al. (2001), Asai (2014).<sup>d</sup> Dispersal mode U: unspecialized, A: animal (attachment or ingestion), W: wind. References: Nakayama et al. (2001), Asai (2014), Tamme et al. (2014).<sup>e</sup> Max height References: Osada (1976, 2002), Satake et al. (1982), Shimizu (2003).<sup>f</sup> 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).<sup>g</sup> Flowering start month References: Satake et al. (1982), Osada (2002), Shimizu (2003), Asai (2014).<sup>h</sup> Flowering end month References: Satake et al. (1982), Osada (2002), Shimizu (2003), Asai (2014). Note that this parameter was not incorporated in the analysis.<sup>i</sup> Life span A: annual or biennial, P: perennial. References: Osada (1976, 2002), Satake et al. (1982), Shimizu (2003).