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Short Communication

Wind dispersal of alien plant species into remnant natural vegetation from adjacent agricultural fields

Chika Egawa

Institute for Agro-Environmental Sciences, NARO, 3-1-3 Kannondai, Tsukuba, 305-8604, Japan

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ABSTRACT

Knowledge regarding the seed dispersal of alien species is crucial to manage invasion risk in fragmented natural habitats. Focusing on wind dispersal, this study assessed the spatial and quantitative extents to which a remnant natural fen receives the seeds of alien species dispersed from adjacent hay meadows in Hokkaido, northern Japan. I established a total of 80 funnel seed traps in the fen at distances of 1, 2, 5, 10, 20, 30, 50, and 100 m from the meadows. The proportion of alien species in the seed rain at each distance was quantified, and the 99th-percentile dispersal distance from the meadows was estimated for each alien species by constructing dispersal kernels. Despite the presence of a marginal ditch and an elevational difference between the fen and the meadows, five alien species, including four grasses that do not have modified seed structures for wind dispersal, dispersed their seeds into the fen. These alien species accounted for up to 65.9% of the seed rain in terms of quantity. The 99th-percentile dispersal distances of the alien species ranged from 3.8 m to 309.3 m, and these distances were longer than the values predicted on the basis of their functional traits, such as terminal velocity. The results of this study demonstrated that numerous seeds of farmland-derived alien species were transported into the remnant vegetation via wind dispersal, and that simple predictions of dispersal distance based on functional traits could underestimate the potential area that alien species can reach. Continuous management both in farmland (to reduce seed escape) and in remnant vegetation (to prevent the establishment of alien species) is necessary to protect native vegetation from biological invasion in agricultural landscapes.
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1. Introduction

The conversion of natural ecosystems into agricultural, industrial, and urban areas has progressed worldwide, resulting in highly divided, fragmented landscapes (Vitousek et al., 1997; Foley et al., 2005). The areas of remnant natural vegetation act as refugia for various plant species, including those that are endangered (Bruun, 2000). Conservation of the remnant vegetation is a pressing matter in maintaining local and regional biodiversity (Hanski and Ovaskainen, 2000; Newbold et al., 2015).

Fragmented natural vegetation, however, often suffers from invasion by undesired alien species from the surroundings, which threaten native flora (Morgan, 1998; Wilkerson, 2013). This is particularly true when the vegetation is surrounded by farmland because farmland generally contains numerous alien weeds (Marshall et al., 2003; Jauni and Hyvönen, 2010). In addition to weeds, cultivated crops themselves can become invasive aliens when they escape from arable fields (Ellstrand

E-mail address: cegawa@affrc.go.jp.

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et al., 2010; Goyal and Sharma, 2016). For instance, imported forage crops, particularly pasture plants, tend to become invasive in natural habitats, and they have a serious impact on the diversity of native species (Lonsdale, 1994; Driscoll et al., 2014). To reduce invasion risk in the remnant vegetation in agricultural landscapes, knowledge of seed dispersal of alien species from farmland into natural habitats is crucial. However, while the occurrence patterns of alien species in remnant fragments have been well documented (e.g., Morgan, 1998; Vilà and Ibáñez, 2011), empirical studies on the processes and extent of their seed dispersal into the fragments are still limited.

Wind is a pivotal dispersal vector for plants (Soons and Bullock, 2008). Because the wind blows continuously across the landscape, wind dispersal would play a key role in the invasion of remnant natural habitats by farmland-derived alien species. Wind dispersal distance is strongly related to plant functional traits, particularly terminal velocity (Tamme et al., 2014). Species possessing modified seed structures for wind dispersal, such as wings, hairs, and pappi, have low terminal velocities and long dispersal distances (Cousens et al., 2008). Species without specific seed structures also disperse their seeds using wind (Quick and Houseman, 2017), but their dispersal distances are relatively short (Jongejans and Telenius, 2001). Predictions of wind dispersal distances using functional traits of alien species are useful for knowing the potential invasion ranges (Thomson et al., 2011; Tamme et al., 2014). However, a recent empirical study using two herbaceous species demonstrated that the distances of wind dispersal for these species measured under natural field conditions exceeded the maximum dispersal distances predicted on the basis of their functional traits (Herrmann et al., 2016). This finding leads to the unfavorable possibility that simple predictions of wind dispersal distances using functional traits can underestimate the area that seeds of farmland-derived alien species can actually reach.

To reveal the extent of the wind dispersal of alien species from farmland into natural habitats, this study quantified the seeds dispersed by wind from hay meadows into an adjacent remnant fen in Hokkaido, northern Japan. I first hypothesized that the remnant fen receives seeds of various meadow-derived alien species via wind dispersal, including those of species lacking morphological adaptations for wind dispersal, and second that the wind dispersal distances of alien species from the meadows are longer than the distances predicted on the basis of their functional traits.

2. Materials and methods

2.1. Study site

The study was conducted in a natural fen in a remnant wetland complex, the Sarobetsu Mire, which is adjacent to recently developed hay meadows in Hokkaido, northern Japan (45°04′N, 141°42′E). The Sarobetsu Mire contains dozens of wetland fragments ranging from 0.5 to 5269 ha in area (Fig. 1; the area calculation was conducted by the author using GIS data from a vegetation map derived from the Biodiversity Center of Japan website: http://www.biodic.go.jp/sarobetsu/download.html, accessed on 30 March 2017). The study fen, ca. 16.6 ha in area, is located in the central part of the largest fragment, which includes mined areas and two lakes, and is designated as a nature reserve in the Rishiri-Rebun-Sarobetsu National Park. The mean annual temperature and annual precipitation in the study year, 2016, measured at the weather station located 6.6 km from the study fen were 5.9 °C and 1004 mm, respectively (Japan Meteorological Agency, 2017). The fen is located in a relatively windy area; the daily mean and maximum wind speed during the study period from June to October 2016 measured at the weather station described above averaged 3.1 ± 1.3 m s^{-1} and 6.2 ± 2.1 m s^{-1} (mean ± SD), respectively, with a peak gust of 23.3 m s^{-1} (Japan Meteorological Agency, 2017). The most frequent wind directions were easterly, south-southwesterly, easterly, and west-southwesterly in June, July, August, and September, respectively.

Grassland-based dairy farming is very common in Hokkaido. The island had 512,100 ha of pastures and hay meadows as of 2013, and these covered 83.5% of the total agricultural grassland area in Japan (Ministry of Land, Infrastructure and Transport, Hokkaido Regional Development Bureau, 2017). The grasses and legumes currently used for pastoral purposes in Hokkaido are all introduced species and were mainly imported from North America and Europe during the Meiji era (1868–1911) to increase forage productivity (Japan Livestock Industry Association, 1976); thus, these pasture plants are all alien species.

In the Sarobetsu Mire, intensive conversion of the wetlands into agricultural lands, mostly pastures and hay meadows, has been conducted since the 1960s (Fujita, 2014). The proportion of wetland areas in the region decreased from 26% to 11%, while that of agricultural lands increased from 10% to 35% during the period from 1947 to 1999 (Ministry of the Environment, Hokkaido Regional Bureau, 2009). The hay meadows adjacent to the study fen were established during the 1980s (Fujita, 1997, 2014). The meadows in this area are fertilized regularly, and the seeds of perennial grasses, mostly those of *Phleum pratense* L. (also known as timothy grass), have been sown as mixtures with the seeds of clovers (Egawa, personal communication). In addition to the intentionally sown species, the meadows contain volunteer grasses and various weeds. During the study period, the meadows were mown twice for hay production, in mid-June (first cut) and late September (second cut). There was a 0.5-m-wide unlined ditch between the fen and the meadows, and the elevation of the fen was 1.0 m higher than that of the meadows (Fig. A.1).

Establishment of various alien species, including pasture plants and agricultural weeds, has been observed in many locations in the Sarobetsu Mire (Fujita, 2014). However, the study fen is likely to be free of these species despite being adjacent to the meadows, because the fen has been dominated by *Sasa* spp. (Tachibana et al., 2013), whose dense cover would inhibit the establishment of shade-intolerant pasture plants and agricultural weeds even if their seeds enter the fen. Therefore, the fen was expected to have no sources of seeds of alien pasture plants and weeds and to be suitable for quantifying the seeds of these species dispersed from the meadows. An experimental plot of 170 m × 100 m was established in the fen (Fig. 1). Prior to the sampling of seed rain, I conducted a floristic survey throughout the whole experimental plot and listed all species found

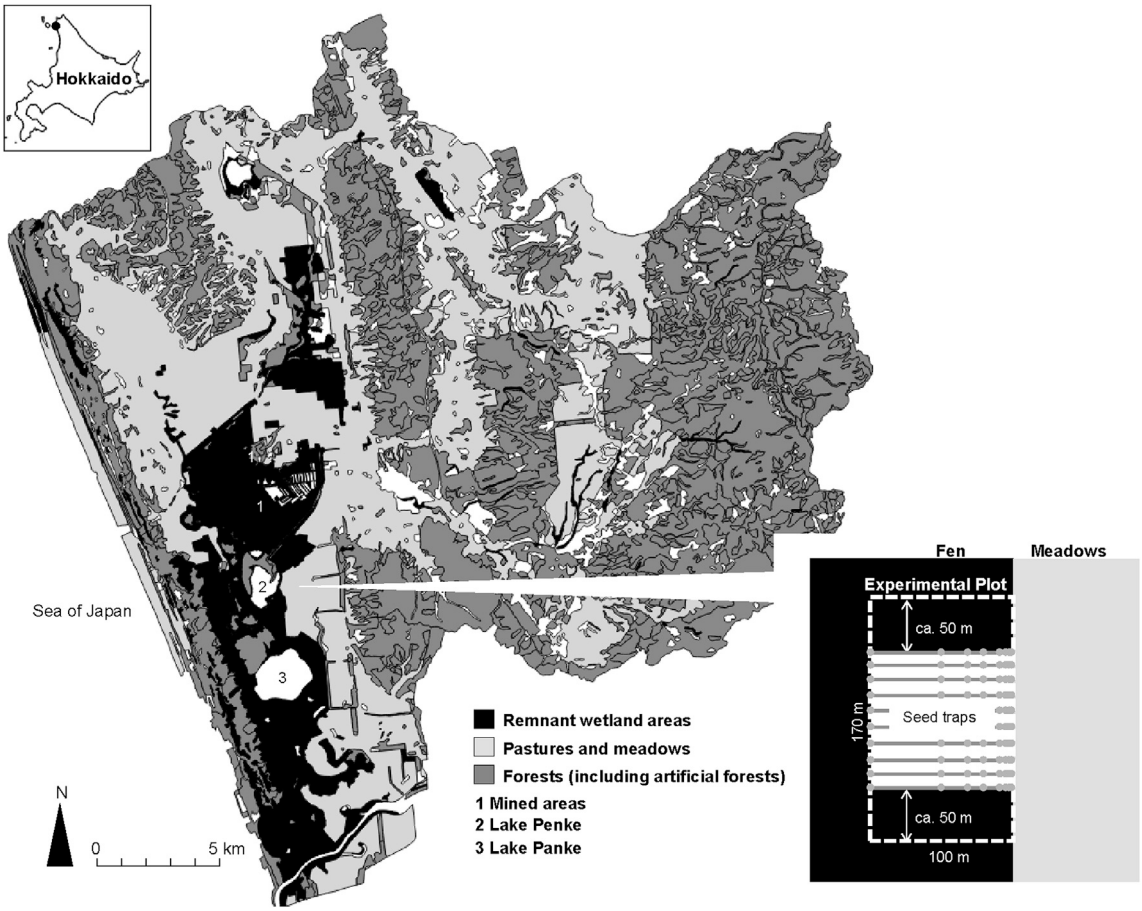

Fig. 1. Location and land use map of the Sarobetsu Mire (areas indicated in black), and a schematic showing the setup of the experimental plot. The exact location of the experimental plot is not shown to protect the personal information of farmers. The land use map was created by the author based on GIS data from a vegetation map derived from the website of the Biodiversity Center of Japan: http://www.biodic.go.jp/sarobetsu/download.html. In the schematic, the scale of the objects is illustrative.

and confirmed that no alien species were established within the plot. I found that the dominant species at the fen edge between the meadows in the experimental plot were *Sasa* spp., *Hydrangea paniculata* Siebold, *Ilex crenata* Thunb. var. *radicans* (Nakai) Murai, *Calamagrostis purpurea* (Trin.) Trin. subsp. *langsdorfii* (Link) Tzvelev, and *Phalaris arundinacea* L.. The abundance of these species except for *Sasa* spp. gradually decreased as the distance from the meadows increased, and the abundance of *Myrica gale* L. var. *tomentosa* C.DC., *Moliniopsis japonica* (Hack.) Hayata, *Phragmites australis* (Cav.) Trin. ex Steud., and *Carex middendorffii* F.Schmidt increased toward the interior of the fen (Table A.1).

2.2. Sampling of the seed rain in the fen

Sampling of the wind-dispersed seed rain in the fen was conducted from 5 June to 10 October 2016; this period covered the main seed dispersal season in the study region (Egawa et al., 2009). In the central part of the experimental plot, 50 m away from the edge, a total of 80 funnel seed traps were established along ten transects that ran perpendicularly to the edge of the unlined ditch that lay between the meadows and the fen (Fig. 1). Because no alien species were established in the experimental plot, it was safe to assume that all the dispersed seeds of alien species in the traps were derived from the meadows. The transects were located on the west side of the meadows. Along each transect, seed traps were placed at distances of 1, 2, 5, 10, 20, 30, 50, and 100 m from the edge of the ditch. Each seed trap consisted of a polyethylene terephthalate (PET) funnel (φ 30 cm, depth 21 cm) with a total sampling area of 706.5 cm^2 and a nylon filter bag attached to the base of the funnel (Fig. A.1). When seeds dropped into the PET funnels, they slipped through the funnels and accumulated in the nylon filters, and never escaped from the traps. The nylon filter bags were covered with plastic plant pots (φ 8 cm, depth 6.5 cm) that had holes in the base to allow water to pass through to protect the captured seeds from damage. The seed traps were attached to robust bamboo sticks and placed at two heights, i.e., 30 cm (low, below the vegetation canopy) and 70 cm (high, approximately the same height as that of the vegetation), above the ground because using different-height traps in combination was expected to increase the probability of seed capture when the seeds were dispersed from various locations (Diacon-Bolli et al., 2013). Five

transects with a total of 40 low traps and another five transects with a total of 40 high traps were established alternately at 5- to 10-m intervals. The traps were emptied three times, in July, August, and October. The sampled seeds were air-dried for at least 10 days before species identification. The seeds were identified under a stereomicroscope using references collected in the field and an illustrated book of seeds by Nakayama et al. (2001), and their weights were then measured. The presence of seed sources, i.e., reproductive individuals, for all captured species was checked both in the fen and in the meadows. To protect the hay materials from physical damage, I was not allowed to enter the meadows, and so the presence of reproductive plants was checked from outside the meadows. The inflorescence height of each sampled species was measured in the fen and at the field margins.

2.3. Estimation of seed dispersal kernels

Dispersal kernels were estimated to explore the potential distance that seeds of alien species can travel via wind from the meadows into the fen. The dispersal data for high and low traps were pooled for each alien species for the analysis. I followed the procedure used by Herrmann et al. (2016) to estimate the dispersal kernels. First, based on the number of seeds collected at each distance, Kaplan–Meier survival curves were constructed using the function *survfit* in R (ver. 3.3.1, R Core Team, 2016), treating the capture of a dispersed seed as an event and the dispersal distances as failure times. Then, dispersal kernels in their one-dimensional form (i.e., probability density functions of the distribution of the dispersal distances) were fitted to the survival curves. Here, three commonly used probability density functions, lognormal, Weibull, and exponential, were tested. The function *optim* in R was used to obtain the maximum likelihood estimates of the parameter values for each of the three probability density functions. Finally, the functions that best fitted the survival curves were determined. I used the Akaike information criterion adjusted for a small sample size (AICc) to select the best-fit functions. The best-fit function, i.e., the dispersal kernel, was obtained for each alien species and for the total alien species based on pooled species information. The 99th-percentile dispersal distance was then calculated from the kernels as an estimate of the potential maximum distance that each alien species can reach.

To compare the wind dispersal distances observed in this study and those predicted on the basis of the functional traits of the plants, the functional-trait-based maximum wind dispersal distance was calculated with 95% confidence intervals on the basis of the growth form, adaptations for wind dispersal, and terminal velocity of each alien species using the predictive model “dispeRsal”, which was developed by Tamme et al. (2014). The terminal velocity values for each species were collected from the LEDA plant trait database (Kleyer et al., 2008).

3. Results

The seed traps captured a total of 632 seeds of 12 species, of which 112 seeds were from five alien species (Table 1). All sampled alien species were agricultural weeds or volunteer pasture grasses that were established in the meadows. The other species captured were native species in the fen. The proportion of alien species in the seed rain was high, particularly at distances of between 1 and 10 m from the meadows, and the proportion reached a maximum of 65.9% in quantity (i.e., the number of seeds) and 57.1% in quality (i.e., the number of species) (Table 1). The seed dispersal seasons of the alien species and the native species clearly differed; the seeds of the alien species were captured mainly in July, while those of the native species were captured in October (Table 1).

Among all alien species, only *Taraxacum officinale* Weber ex F.H.Wigg. had seeds adapted for wind dispersal, and the seeds of this species were captured at the farthest distance from the meadows, 30 m. The remaining four alien grasses did not have specific morphological adaptations for wind dispersal. Out of these four grasses, the number of captured seeds of *Agrostis gigantea* Roth sharply decreased as the distance from the meadows increased, but a decrease was not clear for other alien grasses until the distance reached 20 m. For two native species that were dominant at the fen edge, *H. paniculata* and *C. purpurea* subsp. *langsdorfii*, the number of trapped seeds decreased as the distance from the meadows increased. By contrast, the captured seeds of four native species, *C. middendorffii*, *M. japonica*, *P. australis*, and *Solidago virgaurea* L. subsp. *asiatica* (Nakai ex H.Hara) Kitam. ex H.Hara, increased as the distance from the meadows increased.

Of the three tested dispersal kernel functions, the lognormal distribution fitted best for all cases except for *Anthoxanthum odoratum* L., for which the Weibull distribution was a better fit (Table 2). The estimated 99th-percentile dispersal distance varied among species (Fig. 2), and was farthest for *T. officinale* with pappi (309.3 m from the meadows) and nearest for *A. gigantea* (3.8 m from the meadows). The 99th-percentile dispersal distance for the total alien species exceeded 66 m. For all alien species except *A. gigantea*, the 99th-percentile dispersal distance was longer than the upper bound of the confidence interval of the maximum dispersal distances predicted on the basis of their functional traits (Table 2).

4. Discussion

The results of this study demonstrated that, despite the presence of a marginal ditch and an elevational difference in between, the remnant natural fen receives abundant seeds of alien species from the hay meadows via wind dispersal. The alien species detected were not only the species having morphological adaptations for wind dispersal but also those lacking specific seed structures. This finding supports the expectation that wind dispersal is a pivotal mechanism allowing any farmland-derived alien species to invade remnant vegetation. In addition to wind, other vectors, such as water and animals,

Table 1
The number of seeds captured in each month (J: July, A: August, O: October) and the percentage of alien species at each distance with information on the growth form, status, presence of reproductive individuals (adults), average inflorescence height and seed mass, and adaptations for wind dispersal for each sampled species. In the 'Status'column, W, V, and N indicate weeds, volunteer pasture grasses, and natives, respectively. In the 'Presence of adults' column, M and F indicate the meadows and the fen, respectively.

Species	Growth form	Status	Presence of adults	Inflorescence height (cm)	Seed mass (mg)	Adaptation for wind dispersal	Results at each distance in each month								
							1 m J/A/O	2 m J/A/O	5 m J/A/O	10 m J/A/O	20 m J/A/O	30 m J/A/O	50 m J/A/O	100 m J/A/O	Total
Number of seeds captured															
Alien species															
Agrostis gigantea Roth.	Grass	W	M	42	0.07	None	31/0/0	0/0/1	0/1/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	33
Anthoxanthum odoratum L.	Grass	W	M	40	0.69	None	19/2/0	4/0/0	1/0/0	25/0/0	0/0/0	0/0/0	0/0/0	0/0/0	51
Dactylis glomerata L.	Grass	V	M	68	0.99	None	3/0/0	5/0/0	2/0/0	3/0/0	0/0/0	0/0/0	0/0/0	0/0/0	13
Poa pratensis L.	Grass	V	M	45	0.43	None	0/2/0	0/0/2	2/0/0	1/0/0	0/0/0	0/0/0	0/0/0	0/0/0	7
Taraxacum officinale Weber ex F.H.Wigg.	Forb	W	M	28	0.35	Pappi	3/0/0	2/0/0	0/0/0	0/0/0	1/0/0	2/0/0	0/0/0	0/0/0	8
Total							60	14	6	29	1	2	0	0	112
Native species															
Calamagrostis purpurea (Trin.) Trin. subsp. *langsdorffii* (Link) Tzvelev	Grass	N	F	150	0.06	Hairs	0/13/83	0/3/102	0/3/25	0/0/8	0/0/4	0/0/3	0/0/0	0/1/0	245
Carex middendorffii F.Schmidt	Sedge	N	F	46	1.00	None	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/1/2	0/2/8	13
Hydrangea paniculata Siebold	Shrub	N	F	220	0.03	Wings	0/0/70	0/0/51	0/0/12	0/0/1	0/0/1	0/0/0	0/0/0	0/0/1	136
Moliniopsis japonica Hack.	Grass	N	F	62	1.62	None	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/3	0/0/31	0/0/42	76
Phalaris arundinacea L.	Grass	N	F	150	1.04	None	1/3/1	0/4/1	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/1/1	12
Phragmites australis (Cav.) Trin. ex Steud.	Grass	N	F	180	0.22	Hairs	0/0/1	0/0/1	0/0/5	0/0/6	0/0/2	0/0/6	0/0/4	0/0/9	34
Solidago virgaurea L. subsp. *asiatica* (Nakai ex H.Hara) Kitam. ex H.Hara	Forb	N	F	22	0.30	Pappi	0/0/0	0/0/0	0/0/0	0/0/0	0/0/0	0/0/1	0/0/0	0/0/3	4
Total							172	162	45	15	7	13	38	68	520
Percentage (%) of alien species															
Quantity (No. of seeds)							25.9	8.0	11.8	65.9	12.5	13.3	0	0	17.7
Quality (No. of species)							55.6	55.6	57.1	50.0	25.0	20.0	0	0	41.7

Table 2
Delta AICc values for the three probability density functions fitted to the survival curves for the total and each alien species. The delta AICc values indicate the difference in AICc scores between the model of interest and the best-fit model, which is shown in bold. The 99th-percentile dispersal distances estimated using the best-fit functions, the terminal velocities, and the maximum wind dispersal distances predicted on the basis of functional traits with 95% confidence intervals (CI) are also shown for each species.

	ΔAICc for three probability density functions			99th-percentile dispersal distance (m) estimated using the best-fit function	Terminal velocity (m/s) [a]	Maximum wind dispersal distance (m) with CI (predicted on the basis of functional traits) [b]
	Lognormal	Weibull	Exponential			
Total species	**0.0**	342.51	346.64	66.1	–	–
Each species						
Agrostis gigantea	**0.0**	283.48	138.77	3.8	1.86	2.3 (1.3, 3.9)
Anthoxanthum odoratum	6.79	**0.0**	129.96	41.8	2.38	1.5 (0.9, 2.7)
Dactylis glomerata	**0.0**	3.69	48.33	18.3	2.75	1.2 (0.7, 2.1)
Poa pratensis	**0.0**	3.49	40.59	15.2	2.05	1.9 (1.1, 3.4)
Taraxacum officinale	**0.0**	0.34	19.54	309.3	0.39	28.5 (15.2, 53.6)

[a] According to the LEDA plant trait database (Kleyer et al., 2008).
[b] Calculated using the predictive model "dispeRsal" (Tamme et al., 2014).

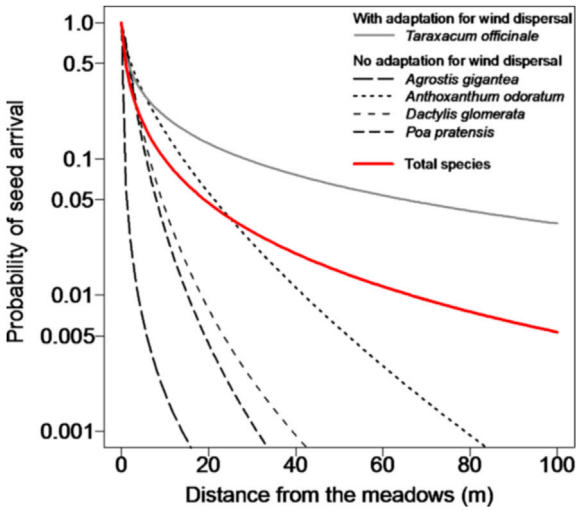

Fig. 2. Estimated dispersal kernels for the total and each alien species. The probability is shown on a log scale.

can contribute to the seed dispersal of alien species from farmland into natural habitats. Kettenring and Galatowitsch (2011) reported the overabundance of agricultural weed seeds in prairie wetlands in corn and soybean agricultural landscapes as a result of the functioning of multiple dispersal vectors. In future studies, the relative importance of each vector in the dispersal of seeds of alien species from farmland into remnant vegetation needs to be clarified for the effective control of invasion risk.

As hypothesized, I found that the observed wind dispersal distances of all species except for *A. gigantea* were longer than the trait-based predictions of maximum dispersal distances. This may be a common occurrence, because Herrmann et al. (2016) also reported that the wind dispersal distances of two herbaceous species measured under field conditions exceeded the trait-based model predictions. One possible factor causing the disagreements between observed and predicted wind dispersal distances is unexpected strong wind sometimes occurring in the field. At the present study site, the daily maximum wind speed averaged 6.2 m s^{-1}, while occasional gusts of up to 23.3 m s^{-1} occurred during the four months of the experimental period. Gusts are known to dramatically increase seed dispersal distances (Nathan and Muller-Landau, 2000; Soons and Bullock, 2008), and the gusts may therefore have been responsible for the observed long-distance dispersal of alien species in this study. In addition to the gusts, mowing activities using large machinery may have somewhat contributed to the long-distance dispersal of the alien species, as combine harvesters and mowers often elongate the seed dispersal distances of agricultural weeds by blowing or scattering their seeds (Antonovics and Ellstrand, 1985; Cousens et al., 2008). The meadows in the study area are harvested using mower-conditioners and sometimes forage harvesters, and such machinery, in combination with strong winds, may have moved the seeds over long distances. The results of this study emphasize that simple predictions of the seed dispersal distance of alien species using their functional traits can underestimate their invasion ranges, which could have serious consequences for the conservation of remnant vegetation. We need more empirical data on the seed dispersal distances of alien species from agricultural fields to adjacent landscapes.

Propagule pressure is the primary determinant of invasion success, and continuous seed dispersal of alien species generally increases invasion risk (Lockwood et al., 2005). In fact, in the Sarobetsu Mire, invasion by pasture plants is occurring in various locations, even though the environments of the wetlands and pastures are different (Fujita, 2014). It is practically

impossible to remove alien species from agricultural lands because alien weeds tend to develop a massive and persistent seed bank in farmlands (Colbach, 2014), and, as is typical for pasture plants, many cultivated crops themselves are introduced alien species (Lonsdale, 1994; Driscoll et al., 2014). Therefore, to protect the remnant vegetation from biological invasion in agricultural landscapes, continuous efforts to remove the seeds of alien species from the vegetation are necessary. For example, in the present study site, the seed dispersal seasons of alien species and native species clearly differed, and this phenological difference could be exploited for the selective removal of the dispersed seeds of alien species from the remnants, for example, by placing seed traps or physical barriers in the vegetation only during the dispersal season of alien species. In addition, efforts to contain the seeds dispersed by alien species within agricultural areas are also indispensable (González-Moreno et al., 2013). For example, to prevent seed escape, it is important to establish the sufficient marginal distance between farmland and natural vegetation based on the dispersal distances of targeted alien species. In conclusion, this study emphasizes the utmost importance of continuous management both in farmland and in remnant vegetation to reduce risk of biological invasion in agricultural landscapes.

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Appendix

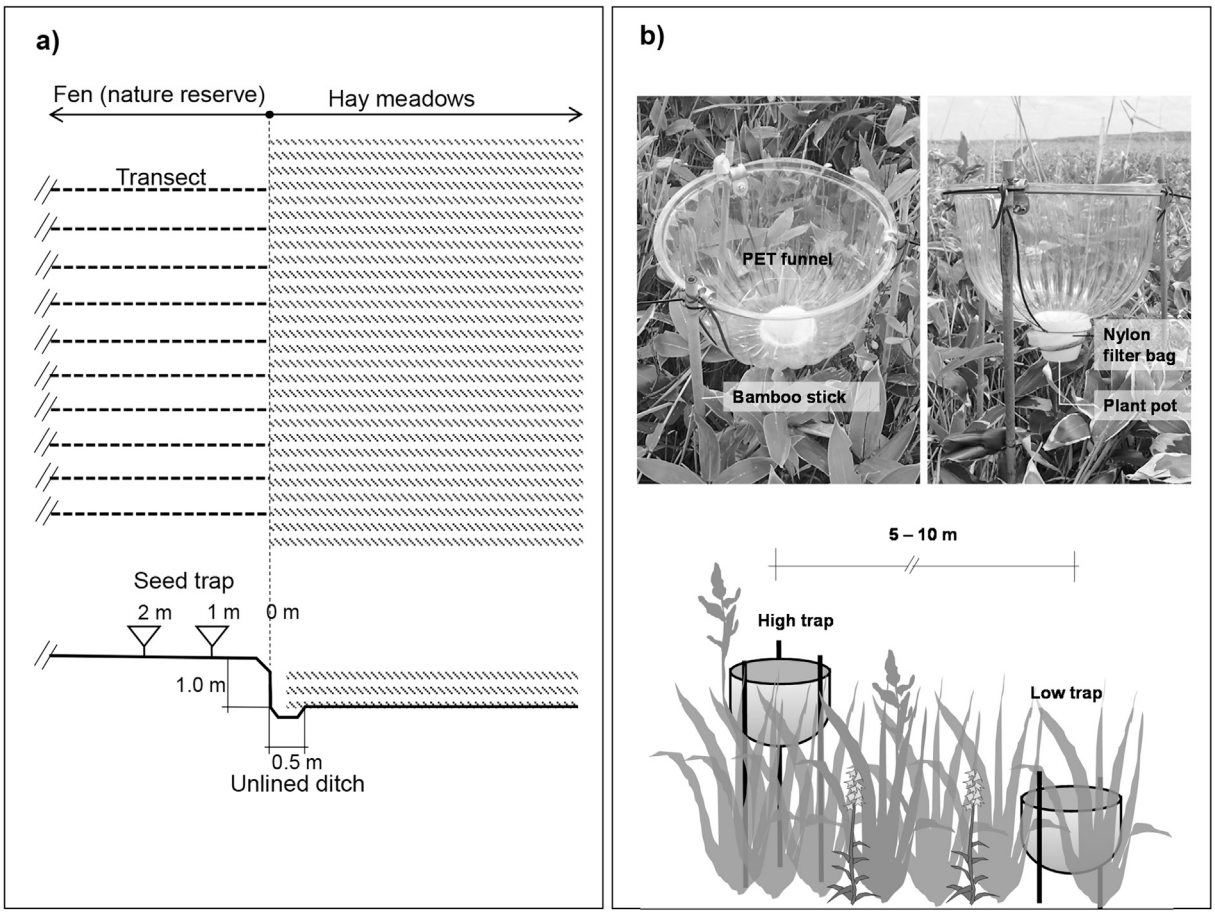

Fig. A.1. a) A schematic showing the experimental setup of the seed traps. Both the scale and shape of the objects are illustrative, as are the locations of the transects. b) The design of the seed traps used in this study.

Table A.1
The list of species found in the experimental plot (170 m × 100 m) in the fen.

Species	Dominant species[a]			Seed trap[b]
	Fen edge	50 m	100 m	
Shrubs				
Empetrum nigrum L. var. *japonicum* K. Koch				
Hydrangea paniculata Siebold	○			○
Ilex crenata Thunb. var. *radicans* (Nakai) Murai	○	○		
Myrica gale L. var. *tomentosa* C.DC.		○	○	
Vaccinium oxycoccos L.				
Orchid				
Dactylorhiza aristata (Fisch. ex Lindl.) Soó				
Grasses				
Calamagrostis purpurea (Trin.) Trin. subsp. *Langsdorfii* (Link) Tzvelev	○	○		○
Miscanthus sinensis Andersson				
Moliniopsis japonica (Hack.) Hayata			○	○
Phalaris arundinacea L.	○			○
Phragmites australis (Cav.) Trin. ex Steud.		○	○	○
Sasa spp.	○	○	○	
Sedges				
Carex middendorffii F.Schmidt			○	○
Eriophorum vaginatum L. subsp. *fauriei* (E.G.Camus) A. et D.Löve				
Juncus decipiens (Buchenau) Nakai				
Forbs				
Artemisia montana (Nakai) Pamp.				
Sanguisorba tenuifolia Fisch. ex Link f. *alba* (Trautv. et C.A.Mey.) Kitam.				
Solidago virgaurea L. subsp. *asiatica* (Nakai ex H.Hara) Kitam. ex H.Hara				○

[a] Five most abundant species in each of three locations, i.e., the fen edge between the meadows, at distances of 50 m and 100 m from the meadows, are indicated with circles as dominant species.
[b] Species whose seeds were captured in the seed traps are indicated with circles.

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