

# Contemporary patterns and temporal changes in alien plant species richness along an elevational gradient in central Japan

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**Background and aims** – Interest in understanding the factors driving change in alien plant species richness along elevation has been increasing. This knowledge assists in understanding the risk of alien plant invasions and the general mechanisms determining species richness patterns in native flora. In addition, recent land use changes within mountainous regions are expected to affect the species richness of alien plants along elevation. However, few reliable datasets have revealed temporal changes in alien species distribution and richness along elevation. In this study, we evaluated regional species richness pattern of alien plants along an elevational gradient compared with that of native plants and assessed the temporal changes in alien plant species richness along elevation in central Japan.

**Methods** – We evaluated the contemporary patterns and temporal changes in alien plant species richness using herbarium records and linked individual-based rarefaction and extrapolation curves.

**Key results** – We showed that alien plant species richness peaks at lower elevations, whereas that of native plants peaks at higher elevation. The estimated alien plant species richness increased over the last approximately thirty years, particularly at the lower elevations. During 1985–2004, eleven of sixteen alien plant species invaded elevations > 2,000 m, whereas until 1976 only two species had colonised elevations > 2,000 m. Earlier invading alien plants have larger elevational ranges than more recent invaders and most alien plants first colonised elevation < 1,000 m.

**Conclusions** – Artificial land use and road lengths are more important for alien plant species richness than total area. We conclude that high propagule pressure and human disturbance support the establishment of alien plant at lower elevation, and then they extend their range. This is reflected in the current patterns and temporal changes in alien plant species richness. Our results suggested that the risk of invasion by alien plants has been increasing in mountain environments.

**Key words** – Alien plant, diversity, elevation, extrapolation, herbarium specimens, invasion, non-native plant, rarefaction, species richness.

## INTRODUCTION

Understanding the mechanism behind geographical variation in species richness is a key objective of ecological and biogeographical research (Sanders & Rahbek 2012). In particular, species richness patterns along elevation in mountainous regions provide important insights into this topic and have attracted considerable attention (Rahbek 1995, Lomolino 2001, Kluge et al. 2006). Elevational gradients are a popular research topic because they provide suitable attributes for understanding the generality of species richness controlling mechanisms. Elevational gradients provide a steep environmental gradient over a relatively short distances and

the numerous studies on this topic worldwide are also useful from the perspective of meta-analysis (Körner 2003, Jump et al. 2009, Sanders & Rahbek 2012). Recently, the interest in alien plant species richness along elevation has increased because of the rapid changes observed in mountain regions caused by tourism and other activities. These changes may increase the risk of alien plant invasions (Pauchard et al. 2009). The steep environmental gradient of elevation additionally provides a useful model system for investigating invasion processes (Arévalo et al. 2005, Becker et al. 2005). Moreover, understanding the spatial patterns of alien species along such gradients could assist in understanding the general mechanisms determining species richness patterns in na-

tive floras (Sax 2001, Alexander et al. 2011). One of the key differences between alien and native plant species richness is the temporal scale driving the patterns of species richness, generally occurring over thousands to millions of years for native plants or endemic plants (Merckx et al. 2015) in comparison to a few hundred years for alien plants (Alexander et al. 2011). In addition, unlike for native plants, anthropogenic disturbance is an important factor promoting alien plant species richness (Gassó et al. 2009, Marini et al. 2009, Moreira-Arce et al. 2015); therefore, recent land use changes within mountainous regions is expected to affect the species richness of alien plants along elevation. However, few reliable data sets have shown temporal changes in the distribution and richness of alien species along elevation, although there is some indication of the range of expansion of alien species (Pauchard et al. 2009).

Alien plant species richness typically shows a decreasing pattern with increasing elevation (Becker et al. 2005, Malen-Cooper & Pickering 2008, Jakobs et al. 2010, Alexander et al. 2011, Barni et al. 2012), although a few surveys have reported hump-shaped patterns with peaks at mid-elevation (Arévalo et al. 2005). The generality in richness patterns and the role of factors in shaping richness patterns along elevation requires assessment for different biogeographical regions (Lomolino 2001, Wu et al. 2013). The comparative approach between climatically analogous regions could provide important insights into the mechanisms of alien plant invasion (Pauchard et al. 2004). In addition, Pyšek et al. (2008) represented the geographical biases present in a study of biological invasions, which highlighted cases of poor research intensity in Asia, and this bias made it difficult to determine the global magnitude of naturalisation in mountains (McDougall et al. 2011). Therefore, it is necessary to evaluate alien plant species richness in mountain regions within Asia. In the current study, we explored the elevational patterns of alien plant diversity in central Japan.

The Japanese archipelago is one of the world's biodiversity hotspots, characterised by high plant diversity and endemism (Mittermeier et al. 2005). However, Washitani (2004) indicated the present status of invasion in Japan by warning that 'Japan is clearly losing against biological invaders, and now stands at a critical moment'. Central Japan is a mountainous region with high plant biodiversity and many steep mountains with high elevation (> 3,000 m), and therefore presents a good case for investigating elevational species richness (Tanaka & Sato 2014). In this region, land area dedicated to urbanisation (built-up elements) has been mainly increasing at lower elevations over the last approximately thirty years, which may result in changes in alien plant species richness (fig. 1); this should be carefully monitored (Barni et al. 2012). However, information regarding alien species distribution and richness along elevation remains limited. Therefore it is necessary to quantify the present status of invasion within the mountainous regions in central Japan and the temporal changes in alien species distribution and richness along elevation. The aims of the current study were: (1) to identify the patterns of species richness of alien plants along elevation in central Japan compared with those of native plants and; (2) to evaluate temporal changes in species richness of alien plants along elevation.

## MATERIAL AND METHODS

### Study area

We surveyed the flora of central Japan, Nagano Prefecture (35.20°N–37.03°N 137.3°E–138.7°E), which is located in the temperate zone, with the study area covering approximately 13,000 km<sup>2</sup> (fig. 1). The elevational span of the study area ranges from 300 to 3,190 m. The mean annual temperature along elevation decreases (12.05°C and -2.63°C at the lowest and highest elevation, respectively), annual precipitation along elevation increases (1,304.9 mm and 2,816.1 mm at the lowest and highest elevation, respectively) (Tanaka & Sato 2014), and the surface area along elevation is highest at 700–900 m (fig. 1A). Area measurements were based on a digital elevation model with a 10-m resolution (Geospatial Information Authority of Japan; <http://www.gsi.go.jp/ENGLISH/index.html>) arranged by the Conservation GIS consortium Japan (<http://cgisj.jp/>). The area of each 100-m elevational belt was calculated using the ArcGIS 10.0 platform (ESRI, Redlands, CA, USA). The forest vegetation in central Japan changes from evergreen broad-leaved forest at low elevations (approximately < 800 m) to deciduous broad-leaved forest at middle elevations (approximately 800 m–1,600 m) and to evergreen coniferous forest at high elevations (approximately > 1,600 m) (Ohsawa 1995).

The area of artificial land use decreases from low to high elevation, and increased from 1976 to 2006 (fig. 1B). The road length is the longest at around 600 m in elevation (fig. 1C). This information was based on a dataset consisting of mesh data with a spatial resolution of 100 m × 100 m and 1 km × 1 km for land use (Land Use Fragmented Mesh in 1979 and 2006) and road length (Road Length Mesh), respectively, obtained from the National Land Numerical Information held by the Ministry of Land, Infrastructure, Transport and Tourism (<http://nlftp.mlit.go.jp/ksj-e/index.html>). We extracted the mesh data of built-up elements from land use mesh data, and then linked the mesh data of built-up elements or road length and elevational data to evaluate elevational patterns of the area of artificial land use and road length using the ArcGIS 10.0 platform (ESRI, Redlands, CA, USA).

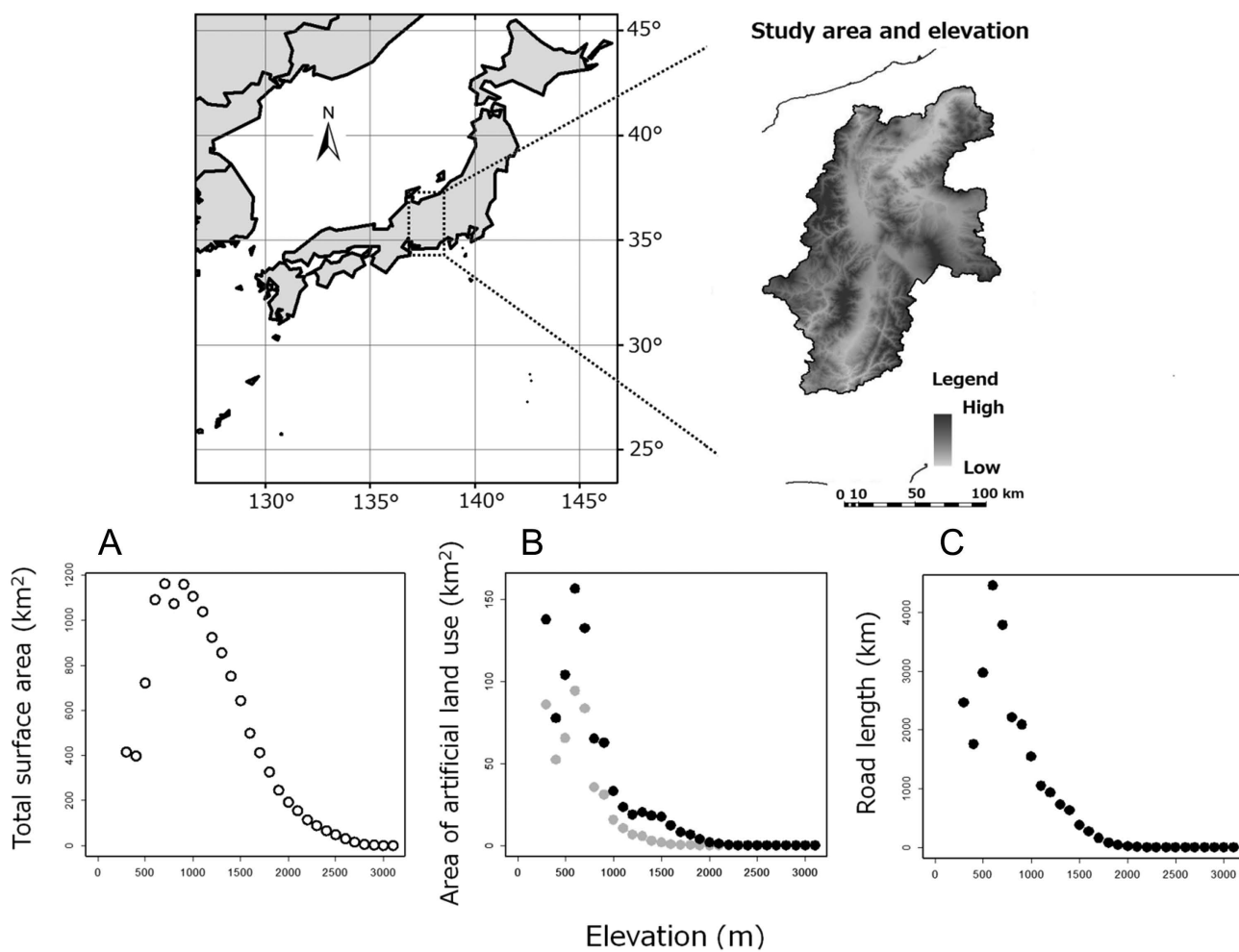
### Data sources

To evaluate regional species richness of alien plants, we used the Nagano Flora database (Kanai & Shimizu 2006, Tanaka & Sato 2014). This database contains > 400,000 data points for vascular plants in this region, including herbarium specimen data and personal observation data until 2004. In the current study, we used only the information related to herbarium specimens of vascular plants with the records of elevation and year to ensure the reliability of information regarding elevation and time. Vascular plant nomenclature conformed to Yonekura & Kajita (2003). Alien/native status was defined according to Shimizu (2003), in which species were classified as alien if introduced since the 1500s. In the current study, the 138,362 specimens with elevation records represented 2,530 species in total, which comprised 2,212 native plants (131,367 specimens) and 318 alien plant species (6,996 specimens). The oldest records of native and alien plants were made in 1875 and 1883, respectively.

### Assessment of total native and alien species richness along elevation

To evaluate the patterns of species richness of alien plants along elevation, we divided the elevational gradient between 300 m and 3,100 m into 29 bands, each of which covered 100 m of elevation (for example, the 300-m elevational band was located between 300 m and 399 m) and integrated the species information into each band. The sampled specimens considerably varied along elevation in this dataset (Tanaka & Sato 2014). To avoid misleading results caused by this sampling bias, we estimated alien plant species richness along elevation using the methods of linked individual-based rarefaction and extrapolation curves (Colwell et al. 2012) up to a sample size of 1,500 individuals to facilitate the comparison of alien plant species richness among elevations. Engemann et al. (2015) showed that rarefaction was the only appropriate method to remove the effect of sampling bias; however, the rarefaction method discards much of the information of larger samples when rarefied species richness is compared because of an adjustment of the sample size to that of the

smallest reference (Colwell et al. 2012). The linked rarefaction and extrapolation curves do not discard data for larger samples using extrapolation up to an equal sample size within a group of samples being compared (Colwell et al. 2012). Because the individuals-based rarefaction curves are recommended to be based on at least twenty individuals (Gotelli & Colwell 2011), we estimated alien plant species richness in elevations with over twenty individuals, which was under 1,900 m. In addition, we estimated native plant species richness along elevation using the linked rarefaction and extrapolation curves up to a sample size of 10,000 individuals for the elevations with sample size under 10,000 individuals, and using rarefaction curves for the elevations with a sample size over 10,000 individuals because of an appropriate sample size for comparing species richness along elevation. Native species richness along elevation was evaluated to adjust the sample size of 10,000 individuals. In the estimation of alien and native plants species richness, we used all records of the same species at one elevation (not one record per species).



**Figure 1** – Location and elevation of the survey area in Japan. The elevational span of the area studied ranged from 300 to 3,190 m. A, total surface area along elevation; B, the temporal change of area of artificial land use along elevation from 1976 (grey fill) and 2006 (black fill); C, the elevational change in road length.

### A comparison of alien with native plants along elevation for certain families

The records of alien species have been infrequent within plant families, for example, the families Asteraceae and Poaceae accounted for approximately one-third of total recorded species (McDougall et al. 2011). These biased records may affect the richness pattern obtained for alien plants, as a pattern including all alien plants may show a characteristic of the family containing most of the alien plants and may not reveal the alien plant itself. Thus, we compared alien and native plants species richness in selected plant families to examine whether the alien species richness along elevation was a general or family specific pattern. When comparing the species richness patterns between alien and native plants, we selected four families, namely Asteraceae, Poaceae, Fabaceae and Brassicaceae. These families were selected as they are characterised by high numbers of species and a high proportion of alien species to total species within the study region (table 1). We did not consider the inconsistency in sampling intensity along elevation in this analysis, as the main aim of the current analysis was to compare elevational species richness patterns of alien and native plants in each family under the same treatment for highlighting similarities or differences in patterns of species richness. To display the trend lines of elevational species richness patterns, we used a one-dimensional curve fitted using Friedman’s smoother (span = 0.3) (Marini et al. 2011, Tanaka & Sato 2013).

To assess the effect of anthropogenic disturbance and propagule pressure in shaping alien plant richness compared with native plant species richness, we used the area of artificial land use (anthropogenic disturbance), road length (propagule pressure) and total area. Total area is one of the major factors related to species richness along elevation (Rahbek 1997, Lomolino 2001), whereas anthropogenic disturbance is an important factor promoting alien plant species richness (Gassó et al. 2009, Marini et al. 2009). We performed simple

**Table 1 – Total, native and alien plant species number of the main plant families in central Japan, and the proportion of alien species to total species.**

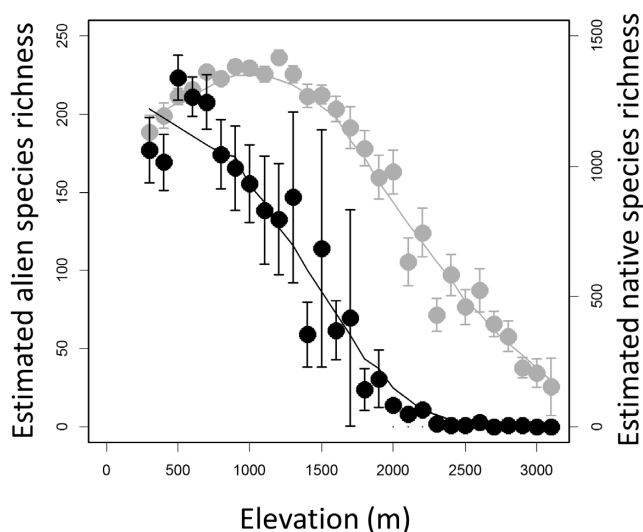
Bold names show the families used in this study.

Family name	Species number			Proportion of alien species
	Total	Native	Alien	
<b>Asteraceae</b>	<b>254</b>	<b>189</b>	<b>65</b>	<b>0.256</b>
<b>Poaceae</b>	<b>245</b>	<b>196</b>	<b>49</b>	<b>0.200</b>
Cyperaceae	196	195	1	0.005
Rosaceae	119	114	5	0.042
Orchidaceae	92	92	0	0.000
<b>Fabaceae</b>	<b>83</b>	<b>58</b>	<b>25</b>	<b>0.301</b>
Lamiaceae	78	71	7	0.090
Ranunculaceae	75	73	2	0.027
Ericaceae	72	72	0	0.000
<b>Brassicaceae</b>	<b>65</b>	<b>35</b>	<b>30</b>	<b>0.462</b>

ordinary least squares (OLS) regression of native and alien plant species richness against the log transformed area of artificial land use, road length and total area. To check the spatial autocorrelation in the estimated species richness and the residuals of OLS regression, we calculated spatial correlograms based on Moran’s *I*. Both the estimated species richness and the residuals of OLS regression showed significant spatial autocorrelation; we additionally performed simultaneous autoregressive models (SAR). The analysis of Moran’s *I* and SAR were performed in SAM v. 4.0 (Rangel et al. 2010).

### An examination of temporal changes in alien plant species richness and distribution

To examine the temporal change in elevational patterns of alien plant species richness, we divided the dataset into two time categories, namely before 1976 (n = 41,934 in total plants and n = 1,485 in alien plants) and 1985–2004 (n = 44,758 in total plants and n = 2,966 in alien plants) to be roughly equal in sampling intensity in total plants. When the alien plant species richness in each elevational band was compared between two time categories, the difference of sampling intensity in each elevation between the two time categories was an issue. Therefore, we estimated alien plant species richness for each elevation with over twenty individuals of alien plants using the linked individual-based rarefaction and extrapolation curves method (Colwell et al. 2012) up to an equal sample size for each elevation between the two time categories (electronic appendix 1). The significance of the difference of alien plant species richness between the



**Figure 2 – Estimated species richness of alien (black circles) and native plants (grey circles) along elevation using the method of linked individual-based rarefaction and extrapolation curves (Colwell et al. 2012) up to a sample size of 1,500 and 10,000 individuals for alien and native plants, respectively. The error bars represent 95% unconditional confidence intervals for estimated species richness. At over 2,000 m in elevation, we showed the observed species richness of alien plants because of a lack of individuals for linked rarefaction and extrapolation curves. Trend lines were fitted with a one-dimensional curve fitted using Friedman’s smoother (span = 0.3).**

two time categories was based on the non-overlap of 95% confidence intervals.

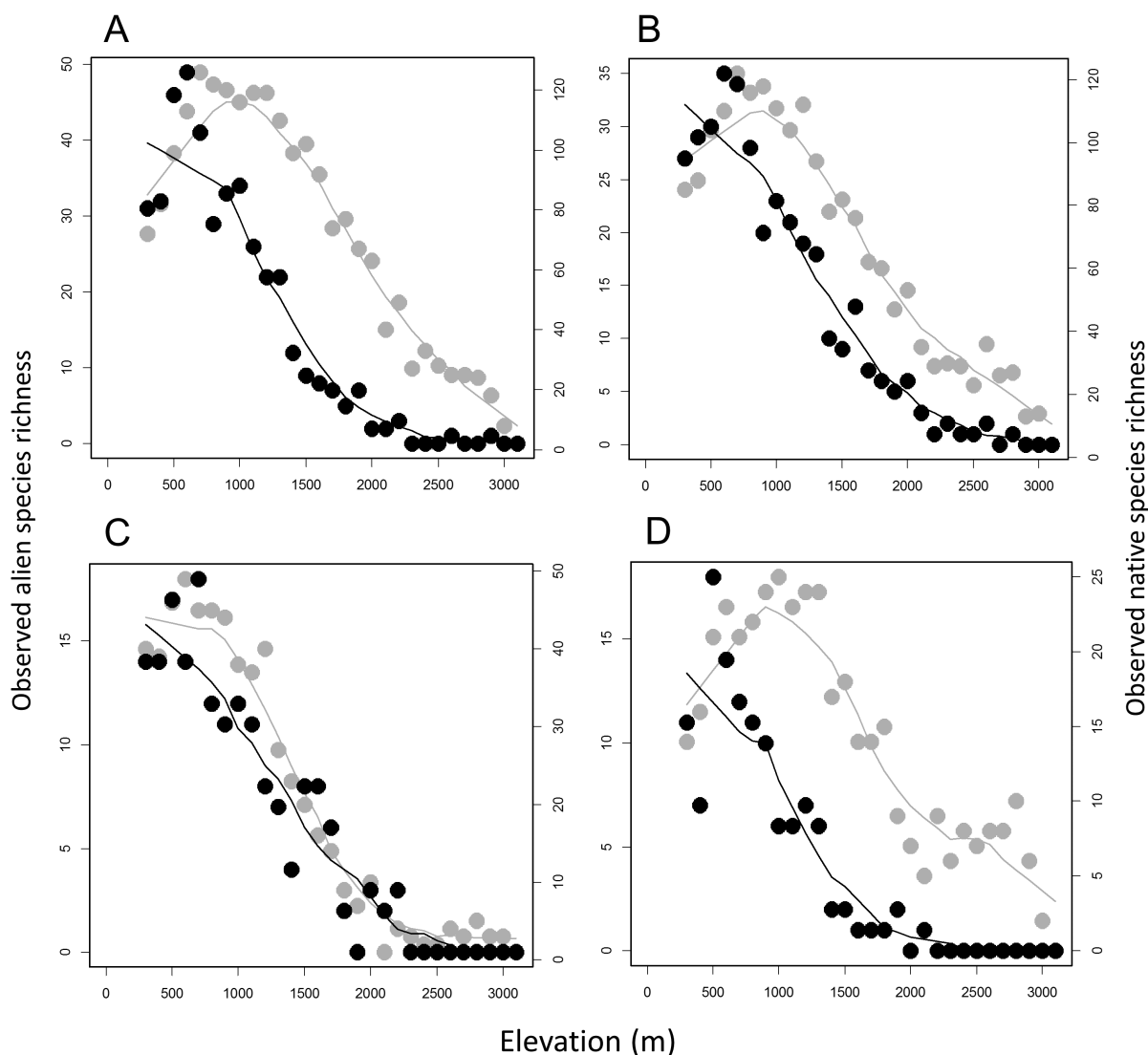
In addition, we performed two analyses to evaluate the temporal change in alien plant distribution. First, we examined the specific temporal changes in maximum elevation for species richness presented in each time category with the top 10% of the number of specimens (sixteen species). We performed a Wilcoxon signed-rank test for assessing the temporal changes in maximum elevation for sixteen species. Lastly, we examined the relationship between minimum residence time (first corrected year in this region) and elevational range of alien plants to test the effect of residence time (Rejmánek 2000, Wilson et al. 2007, Haider et al. 2010). We performed OLS regression of minimum residence time against the elevational range of all alien plants. In addition, we checked the records of elevation that each alien plant species corrected

first. Statistical analyses were performed using R 2.14.0 for Windows (R Development Core Team 2009) and the linked rarefaction and extrapolation curves were computed with Estimate S9 (Colwell 2013).

## RESULTS

### Native and alien species richness along elevation

The estimated species richness of total alien plants along elevation showed a decreasing pattern with a peak at 500 m in elevation, whereas that of total native plants showed a hump-shaped pattern, with a peak at the higher elevation of approximately 1,100 m (fig. 2). Species richness of alien plants in selected families declined with increasing elevation (fig. 3). In contrast, the native plant species richness within the fami-



**Figure 3** – Observed species richness of alien (black circles) and native plants (grey circles) along elevation in four selected families; A, Asteraceae; B, Poaceae; C, Fabaceae; D, Brassicaceae. Trend lines were fitted with a one-dimensional curve fitted using Friedman's smoother (span = 0.3).

lies Asteraceae, Poaceae and Brassicaceae showed peaks in species richness at higher elevations than those of alien plants. Only in Fabaceae did both alien and native species richness show the same decreasing patterns with increasing elevation.

The log transformed area of artificial land use and road length explained the variation in alien plant species richness ( $R^2 = 0.927$ ,  $P < 0.001$ ;  $R^2 = 0.865$ ,  $P < 0.001$ , respectively) in OLS regression and (pseudo- $R^2 = 0.927$ ; pseudo- $R^2 = 0.863$ , respectively) in SAR. The log transformed area of artificial land use explained more variation in alien plant species richness than that in native species richness ( $R^2 = 0.786$ ,  $P < 0.001$ ) in OLS regression and (pseudo- $R^2 = 0.784$ ) in SAR, whereas the log transformed total area explained less variation in alien plant species richness ( $R^2 = 0.544$ ,  $P < 0.001$ ) in OLS regression and (pseudo- $R^2 = 0.409$ ) in SAR than that in native species richness ( $R^2 = 0.900$ ,  $P < 0.001$ ; pseudo- $R^2 = 0.888$ , respectively).

### An examination of temporal changes in alien plant species richness and distribution

The total alien plant species richness in the region of the current study was estimated to have increased by 55 species between the period up to 1976 (243 species) and the period 1985–2004 (298 species) using the method of linked individual-based rarefaction and extrapolation curves up to 6,000

individuals (fig. 4A). Along the elevational gradient, alien plant species richness at four elevations (500, 600, 700 and 1,000 m) increased significantly between the two temporal periods evaluated (fig. 4B).

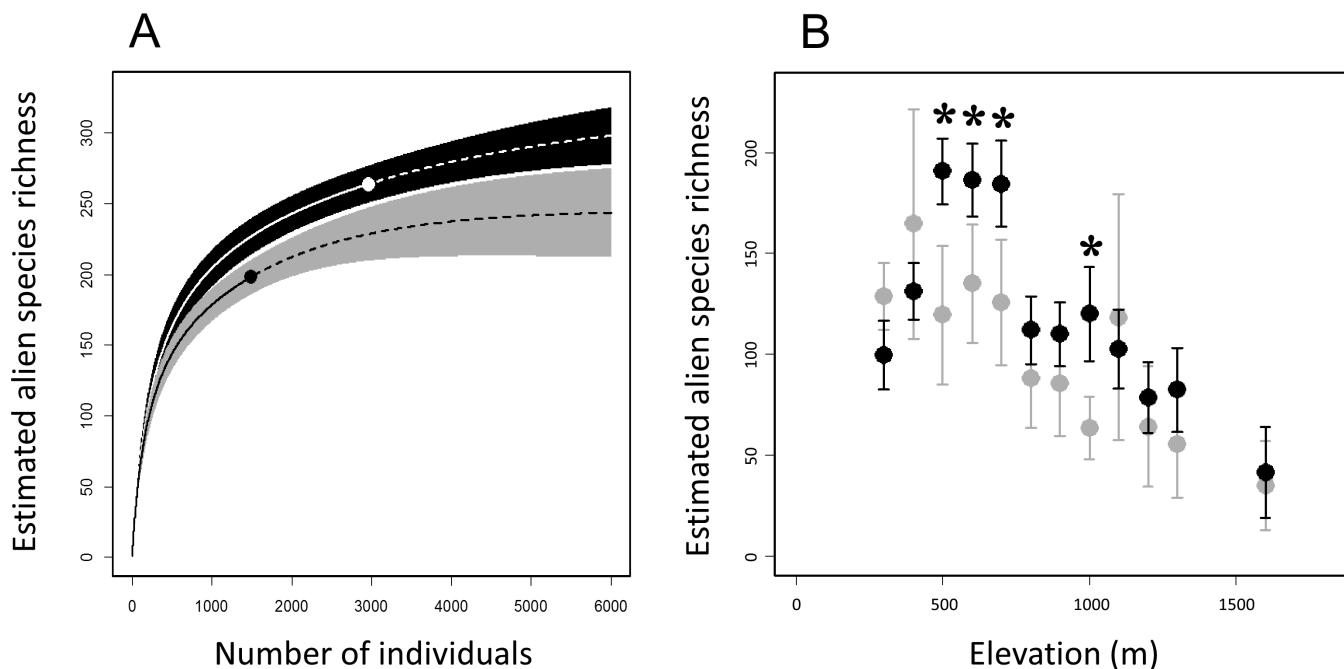
The maximum elevation of the sixteen species increased (Wilcoxon signed-rank test,  $P = 0.00195$ ) at an average of 362.5 m between the two time periods. The maximum elevation of *Agrostis gigantea* remarkably increased (1,000 m; from 1,800 to 2,800 m), followed by *Taraxacum officinale* (900 m; from 1,300 to 2,200 m) and *Oenothera biennis* (700 m; 1,300 to 2,000 m) (table 2).

There was a positive relationship between minimum residence time and elevational ranges ( $R^2 = 0.321$ ,  $P < 0.001$ ) (fig. 5A); alien plant species that invaded earlier had larger elevational ranges than recent invaders. In addition, the first corrected elevation of each alien plant species concentrated at around 600 m (fig. 5B) and a large proportion of alien plant species was introduced < 1,000 m in elevation.

## DISCUSSION

### Native and alien species richness along elevation

In the current study, we estimated species richness patterns of alien plants along elevation using herbarium specimens compared with those of native plants and assessed the temporal change of alien plant species richness along elevation.

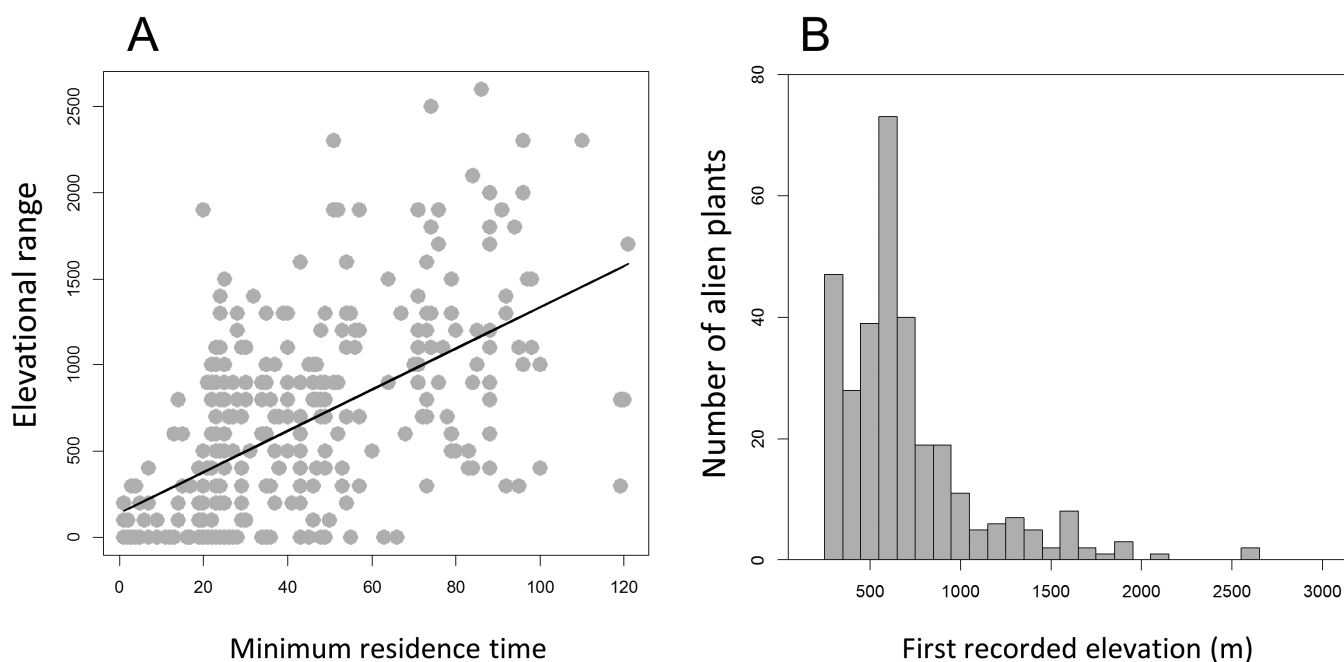


**Figure 4** – The temporal changes in: A, total alien plants in central Japan; and B, estimated species richness of alien plants along elevation. In the temporal changes in total alien plants, linked individual-based rarefaction (filled black circle; solid lines) and extrapolation (dotted lines) curves with 95% unconditional confidence intervals for alien plant species up to a sample size of 6,000 individuals based on herbarium specimens until 1976 (grey fill) and 1985–2004 (black fill). In the temporal changes in alien plants along elevation, grey and black filled circles represent estimated species richness until 1976 and 1985–2004, respectively, using the method of linked individual-based rarefaction and extrapolation curves (Colwell et al. 2012) up to equal sample size for each elevation. The error bars represent 95% unconditional confidence intervals for estimated species richness. Asterisk represents significant difference ( $P < 0.05$ ) based on non-overlap of 95% confidence intervals.

**Table 2 – Specific temporal changes of maximum elevation for alien plants presented in each time category with the top 10% of number of specimens.**

The number in parentheses shows the number of specimens in each time category.

Family	Species name	Maximum elevation	
		until 1976	1985–2004
Poaceae	<i>Agrostis gigantea</i>	1,800 (35)	2,800 (56)
	<i>Schedonorus phoenix</i>	1,500 (36)	2,100 (52)
	<i>Dactylis glomerata</i>	1,600 (26)	2,000 (51)
	<i>Poa pratensis</i>	2,000 (38)	2,000 (30)
	<i>Phleum pratense</i>	2,300 (45)	2,000 (21)
Asteraceae	<i>Erigeron annuus</i>	1,900 (42)	2,200 (78)
	<i>Erigeron canadensis</i>	1,400 (16)	1,200 (64)
	<i>Taraxacum officinale</i>	1,300 (26)	2,200 (37)
Polygonaceae	<i>Rumex obtusifolius</i>	1,500 (25)	1,600 (63)
	<i>Rumex acetosella</i>	1,900 (35)	2,200 (40)
Fabaceae	<i>Trifolium pratense</i>	1,600 (10)	2,200 (59)
Caryophyllaceae	<i>Stellaria media</i>	1,600 (26)	2,200 (43)
Lamiaceae	<i>Lamium purpureum</i>	1,400 (18)	1,400 (50)
Amaranthaceae	<i>Amaranthus hybridus</i>	900 (16)	1,400 (47)
Plantaginaceae	<i>Veronica arvensis</i>	1,100 (23)	1,400 (58)
Onagraceae	<i>Oenothera biennis</i>	1,300 (15)	2,000 (64)

**Figure 5** – A, elevational range of alien plant species regressed on their minimum residence time. The regression lines were fitted using OLS regression ( $R^2 = 0.321$ ,  $P < 0.001$ ); B, histogram of first recorded elevation of alien plant species.

We showed a regional peak in total alien plant species richness and within selected families at lower elevations (figs 2 & 3). This result agrees with those of previous studies in local alien plant species richness based on field inventories (Becker et al. 2005, McDougall et al. 2005, Jakobs et al. 2010, Alexander et al. 2011, Barni et al. 2012) and regional alien plant species richness based on literature and scientific collection (Marini et al. 2013, Dainese et al. 2014), which indicated that the peak of species richness of alien plants at lower elevations is a more general pattern in regional or local species richness and in total species and within specific families.

When comparing species richness patterns among taxonomic groups along the same elevational gradient, the richness pattern or richness peaks were generally different (Rahbek 1995, Kessler 2000, Krömer et al. 2005, Grau et al. 2007). The species richness patterns of native plants are known to be shaped not only by climatic (Kluge et al. 2006, McCain 2007, Kessler et al. 2011) and spatial factors (Rahbek 1997, Sanders 2002, Romdal & Grytnes 2007), but also by evolutionary and historical factors (Wiens et al. 2007, Kluge & Kessler 2011, Graham et al. 2014). The optimal climate among taxonomic groups varies due to specific climatic requirements, reflecting evolution, which leads to differences in species richness patterns and peaks. However, the alien plants in the current study showed similar patterns and peaks among the four families, while peaks for native plants differed among families. This result confirmed that the species richness of alien plants was more affected by pre-adaptation to climate (e.g. lowland introduction filter), anthropogenic influence and dispersal processes (e.g. propagule pressure) than evolutionary or historical factors (Becker et al. 2005). In fact, although area is a crucial variable that determines patterns of biodiversity (Rahbek 1997, Lomolino 2001), in alien plants, the area of artificial land use and not total area was more influential for regional species richness patterns of alien plants than for native plants, which explains the difference between alien and native species richness along elevation. In addition, most alien plant species were first introduced < 1,000 m in elevation, as illustrated by the first corrected elevation of alien plants (fig. 5B). We found a highly significant relationship between estimated alien species richness and artificial land use or road length. Our results showed the importance of the property factors driving alien plant species richness, such as the lowland introduction filter and anthropogenic influence.

#### **An examination of temporal changes in species richness and distribution of alien plant species**

The temporal changes in alien plant species richness along elevation showed increasing species richness at lower elevations (500, 600 and 700 m) (fig. 4). This is because of the fact that these elevations are affected by high propagule pressure (long road length and increasing artificial area) (Colautti et al. 2006, Seipel et al. 2012). This result additionally supported the peak in species richness of alien plants at lower elevations. One of the remarkable results of the current study is that alien plant species richness increased at 1,000 m, which experienced relatively lower propagule pressure than lower elevations (500, 600 and 700 m) and a high spe-

cies richness of native plants. Furthermore, most alien plants were first introduced < 1,000 m in elevation and there is a positive relationship between minimum residence time and elevational ranges (fig. 5A). These results suggested that alien plant species in this area first invaded at lower elevations along the road systems as a result of the high propagule pressure (Alexander et al. 2011). This is followed by an extension of their distribution range (Alexander et al. 2011), subsequently spreading to the montane region in central Japan. An additional potential explanation for this result is climate change. In this region, the forest class along increasing elevation changes from evergreen, broad-leaved forest to deciduous, broad-leaved forest, with the boundary located at approximately 900 m (Ohsawa 1995). The assembly of ferns and lycophytes additionally changes at this boundary, coinciding with the upper elevational limits of fern distribution (Tanaka & Sato 2013). This elevational boundary of woody vegetation and fern assembly is determined by temperature conditions (Ohsawa 1995, Tanaka & Sato 2013). Thus, the results indicating increasing alien species diversity at 1,000 m over the key elevation boundary of 900 m and the increasing upward trend may be driven by climate change (Dukes & Mooney 1999, Wilson et al. 2005, Walther et al. 2009). In addition, the maximum elevation of sixteen species presented in both time categories increased at an average of 362.5 m and eleven of sixteen alien species invaded areas > 2,000 m during the period 1985–2004, whereas only two species reached areas > 2,000 m prior to 1976 (table 2). This augmentation is probably caused by selection for genotypes that are phenotypically more plastic due to ecological filtering (Haider et al. 2011) and because of climate change (Wilson et al. 2005, Walther et al. 2009). These results indicated that the risk of invasion by alien invasive plants has been increasing not only in the mountainous regions but also in the subalpine zone in central Japan.

In the current study, we determined only whether or not estimated alien plant species richness could increase between the two temporal periods along elevation. We were unable to estimate the absolute value of increased alien species richness; thus, we could not elucidate the factors related to the upward trend of alien plant distribution and did not quantify the impacts of land use or climate change on increased alien plant species richness. However, the process whereby an alien plant first invades a lower elevation with high propagule pressure and anthropogenic influence and then extending its distribution range is reflected in their current patterns and temporal changes in alien plant species richness along elevation. In addition, our results suggest that the risk of invasion by alien invasive plants has been increasing in mountainous environments in this region and highlight the necessity of quantification of the effects of land use changes or climate changes along elevation on the dynamics of alien plant species.

#### **The utility and disadvantages of using herbarium records**

In the current study, the patterns of species richness and temporal changes for alien plants were based on herbarium records. Herbarium specimens are an important resource for



studies of biodiversity (Shaffer et al. 1998) and primary distribution databases have recently been highly utilised in macroecological studies. Herbarium specimens and databases of alien plants additionally provide important information regarding invasion phenomena (Fuentes et al. 2013). However, many studies highlighted sampling bias when using herbarium records to assess species richness patterns. For example, the number of records and documented species were strongly correlated and biased sampling efforts or under-sampling may provide misleading results when evaluating spatial patterns of biodiversity (Hortal et al. 2007, Grytnes & Romdal 2008, Yang et al. 2013, Tanaka & Sato 2014). To reduce this sampling bias in the current study, we used the linked individual-based rarefaction and extrapolation curves, which is a suitable method to avoid sampling bias (Engemann et al. 2015), and evaluated valid species richness patterns of alien plants along elevation. However, alien plant specimens were fewer than those of native plants in the database used. The range of 95% confidence intervals in estimated species richness of alien plants extended wider at 1,500 m and 1,700 m in elevation than that at other elevations (fig. 2). This extension of the confidence interval resulted from the low sampling intensity at these elevations, which blurred the exact estimated species richness.

In the evaluation of temporal changes in alien plant species richness using herbarium records, other sampling bias, such as non-random sampling biases over time, may occur (Delisle et al. 2003, Crawford & Hoagland 2009). Thus, the increase in alien plant species richness may simply result from an increase in the collecting effort over time. In the current study, we compared two time categories to contain roughly equal sampling intensity for total plants to reduce the sampling bias over time. Thus, the approximately two fold increase in the number of herbarium records of alien plants between the two time categories (see the Method section) might not be a result of the high sampling intensity during the period 1985–2004, but rather of the increasing numbers of alien plant species invading central Japan. In fact, the estimated species richness using the linked individual-based rarefaction and extrapolation increased between the two time categories (fig. 4A).

When evaluating the contemporary biodiversity and the temporal changes in species distribution, community structure and species richness using herbarium records, not only the sampling biases mentioned above, but also other kind of biases, namely taxonomic and geographical sampling biases (Crawford & Hoagland 2009), are inevitable. These taxonomic and geographical sampling biases could not be avoided when evaluating the spatial patterns and temporal changes in species richness; however, the continuous accumulation of herbarium records may reduce these biases due to the saturation of records. Thus, a long history of herbarium collection is necessary to assess plausible results (Pyšek & Prach 1993, Crawford & Hoagland 2009). The database used in the current study did not include more recent information of alien plant species richness because of a lack of recent herbarium specimens of alien plant species. Thus, it is necessary to accumulate herbarium specimens from mid-elevation to high-elevation, to update this database and to survey local patterns of species richness based on a plot sampling for evaluating

and monitoring species richness of alien plant along elevation. Recent records of alien plants will facilitate the evaluation of regional spatial patterns and temporal changes in alien plant species richness and could develop a spatial pattern of alien plants and invasion phenomena.

#### SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, supplementary data site (<http://www.ingenta-connect.com/content/botbel/plecevo/supp-data>) and consist of a table of individuals of alien plants and sample size for linked individual-based rarefaction and extrapolation curves along elevation.

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