

Historical impacts on linear habitats: the present distribution of grassland species in forest-edge vegetation

Tomoyo KOYANAGI ^a, Yoshinobu KUSUMOTO ^b, Shori YAMAMOTO ^b, Satoru

5 OKUBO ^a, Kazuhiko TAKEUCHI ^a

^a Department of Ecosystem Studies, Graduate School of Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

E-mail addresses: aa077131@mail.ecc.u-tokyo.ac.jp (TK),
aokubos@mail.ecc.u-tokyo.ac.jp (SO), atake@mail.ecc.u-tokyo.ac.jp (KT)

10 ^b Biodiversity Division, National Institute for Agro-Environmental Sciences, 3-1-3, Kannondai, Tsukuba, Ibaraki 305-8604, Japan

E-mail addresses: kusu@niaes.affrc.go.jp (YK), shori@affrc.go.jp (SY)

Correspondence: T. Koyanagi, Department of Ecosystem Studies, Graduate School of
15 Agricultural and Life Sciences, The University of Tokyo, 1-1-1 Yayoi, Bunkyo, Tokyo 113-8657, Japan

E-mail address: aa077131@mail.ecc.u-tokyo.ac.jp

Phone number: (+81)-3-5841-5052, Fax number: (+81)-3-5841-5072

Abstract

In highly fragmented agricultural landscapes, abandoned forests and dense coniferous plantations established on former semi-natural grassland remain potentially suitable sites for the restoration of grassland communities. The roadside vegetation along the edges of these remnant forests could be a key landscape component, because these communities retain pools of grassland species that are maintained by regular mowing alongside public roads to improve traffic safety. We evaluated the effect of land-use history and the proportion of suitable surrounding habitats on the present distribution of grassland species in roadside forest-edge vegetation. The average number of grassland species was significantly lower at sites that had been cultivated since the 1950s, but it did not differ between uncultivated sites and sites cultivated during the 1880s. Positive effects of the proportion of suitable habitats around the sites were detected at specific spatial scales (500- and 700-m squares), and these effects were indistinct at sites that had lost populations to cultivation. In addition to the present habitat conditions (e.g., forest type), the best-fit model for explaining the present distribution of grassland species at a site included both the site's land-use history and the past proportion of suitable habitat around the sites. Even in remnant linear habitats such as forest-edge vegetation along roads, historical patterns of site conditions and the

landscape matrix at optimum scales can provide useful knowledge to improve explanations of the present distributions of grassland species. These information can help identify abandoned or planted forest sites potentially suitable for restoration with grassland species.

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Keywords: semi-natural grassland; land-use history; habitat fragmentation; roadside; restoration; *satoyama* landscape

Introduction

Linear landscape elements, such as those colonized by roadside vegetation, may compensate for losses of grassland species in the surrounding landscape by serving as refugia or reservoirs for these species (Tikka et al., 2000, 2001; Cousins, 2006).

5 Although the community structures or species compositions at these sites differ from those of semi-natural grassland (Tikka et al., 2000; Jantunen et al., 2006), roadsides can nonetheless function as key habitats because of their important role as potential seed sources for adjacent restored sites (Soons et al., 2005). The potential for restoration of grassland habitats after the abandonment of other forms of intensive land use depends

10 strongly on seed source limitations in the aboveground vegetation and surrounding areas (e.g., Pärtel et al., 1998; Walker et al., 2004; Bisteau and Mahy, 2005). In Japan, semi-natural grassland was one of the main components of the traditional *satoyama* agricultural landscape (Takeuchi, 2003; Ichikawa et al., 2006). However, land-use changes such as urbanization, conversion of grassland into cropland, abandonment, and

15 establishment of tree plantations over the past century have posed a major threat to grassland species diversity. Especially in the *satoyama* landscapes surrounding metropolitan areas, only limited numbers of semi-natural habitats for grassland species remain, mostly in areas under regular management on public property (Sakiyama and Itoga, 1994). Abandoned deciduous or mixed forests and dense coniferous plantations

established at former semi-natural grassland sites remain potentially suitable sites for the reestablishment of grassland species. The roadside vegetation along the edges of these remnant forests could be a key reservoir of these species, because this vegetation retains pools of grassland species that have been maintained by the regular management (mowing) that occurs along public roads to improve traffic safety.

A number of recent studies have argued that historical knowledge of sites and their surrounding areas is required to understand the present species distribution in a landscape (e.g., Bruun et al., 2001; Cousins and Eriksson, 2001; Eriksson et al., 2002; Alard et al., 2005; Gustavsson et al., 2007; Pärtel et al., 2007; Johansson et al., 2008). Knowledge of the long-term dynamics of species distribution, obtained from studies that focus on historical human activities, is essential for effective conservation planning (Foster et al., 2003; Lunt and Spooner, 2005). However, whether these historical impacts can be recognized in remnant linear habitats such as roadsides is still unclear. If we can recognize the relationships between the present distribution of grassland species and historical human activities, even in the highly disturbed forest-edge vegetation along roads, we may be able to identify useful knowledge for identifying the potential for restoration of grassland species in these abandoned or planted forests and for targeting sites for future restoration.

Historical factors determine large-scale processes such as the migration of

species between regions and the dispersal of species between and within local populations (Zobel, 1997). Human land use has affected these processes by changing both the environmental conditions at sites and the spatial patterns of the habitats around these sites. For example, a long continuity of regular management of a site has an
5 important influence on the current species richness (Cousins and Eriksson, 2002; Johansson et al., 2008), and positive effects of management can be recognized even in small remnant areas such as mid-field islets in highly fragmented landscapes (Cousins and Eriksson, 2002). On the other hand, conversion of land into cropland has negative impacts on grassland species because it changes the soil properties and eliminates both
10 aboveground seed sources and seeds in the soil seed bank (Bakker and Berendse, 1999; Walker et al., 2004). The trajectory of recovery after the cessation of cultivation depends strongly on the levels of abiotic and biotic constraints; under the impact of modern agriculture, unassisted recovery to the desirable species composition and community structure is almost impossible (Cramer et al., 2008). Recent studies have
15 demonstrated the impacts of historical changes in the landscape structure around sites, and they have revealed empirical relationships between the present grassland species diversity and the habitat connectivity more than 50 years ago (Lindborg and Eriksson, 2004; Helm et al., 2006; Cousins et al., 2007). Because of the species relaxation process, which has also been identified in other taxa (Saunders et al., 1991; Debinski and Holt,

2000; Gonzales, 2000; Ewers and Didham, 2006), the distribution patterns of grassland species are not necessarily related to the present habitat area and connectivity. Although species may respond slowly to habitat fragmentation, sometimes over periods as long as a century, previous studies have produced inconsistent results (e.g., Krauss et al., 2004; 5 Piessens et al., 2004; Adriaens et al., 2006). In addition, the time periods and spatial scales that are important for explaining present diversity patterns remain unclear, because most studies have evaluated such effects at only one specific temporal or spatial scale (but see Krauss et al., 2004; Lindborg and Eriksson, 2004; Lindborg, 2007). By simultaneously comparing the effects of landscape structures in different time periods 10 and at different spatial scales among sites with different land-use histories, the relative importance of historical changes at and around a site could be clarified.

Our objectives were therefore to (1) identify the impacts of present site conditions and past land use on remnant linear forest-edge vegetation along roads; (2) identify how past surrounding landscape has had different effects on the present 15 distribution of grassland species in forest-edge vegetation with different land-use histories; and (3) reveal the relative importance of historical information at sites and in their surroundings for explaining the present diversity and pattern of grassland species in these remnant linear vegetation areas. This knowledge could provide useful tools for selecting conservation and restoration targets for grassland species in *satoyama*

landscapes.

Methods

Study area

5 The study area was located in the Tsukuba–Inashiki upland region, which lies in the northeastern part of Japan’s Kanto Plain. The altitude ranges from approximately 20 to 30 m above sea level. The Tsukuba–Inashiki upland is a diluvial upland overlain by immature soils derived from aeolian volcanic ash or tephra called the Kanto Loam layer. The mean annual temperature is 13.5°C, and the mean annual precipitation is
10 approximately 1230 mm (Japan Meteorological Agency, 2007).

Semi-natural vegetation and traditional management

The vegetation of the semi-natural grasslands found in this region belongs to the *Pleioblastus chino* – *Miscanthus sinensis* phytosociological community (Miyawaki,
15 1980). Human activities have prevented succession of these grasslands into the region’s potential climax vegetation, which is a mixed evergreen–broadleaved forest for many centuries. Two main types of semi-natural habitats for grassland species have been maintained by the traditional agricultural system (Kamata and Nakagoshi, 1990). One is open semi-natural upland grassland or shrubland, which represents common lands

located at the same distance from each village that were mown in early winter almost every other year. *Miscanthus sinensis* dominates this kind of extensively managed semi-natural grassland, but there are many subordinate grassland species; Miyawaki (1980) reported that almost 40 typical grassland species coexisted. The second type of habitat is open secondary forests, which consist mainly of *Quercus acutissima*, *Quercus serrata*, and *Pinus densiflora*. People typically cut these trees once every 20 to 30 years and also mowed the understory layer to produce organic fertilizer or livestock feed. The traditional management in these forests maintained high light availability, so the species compositions in the understory remained similar to those of the open semi-natural grassland or shrubland (Fujii and Zinnai, 1979; Yamamoto and Itoga, 1988).

Land-use history

The two types of semi-natural habitats for grassland species were widely distributed in the study area in the 1880s. The source of these data will be discussed in the next section. There are two major causes of the dramatic land-use changes that have occurred during the past 100 years in this region (Sakiyama and Itoga, 1994). From the 1880s to 1950s, almost all of the semi-natural grassland that was widespread in upland areas disappeared and became cropland or open *P. densiflora* forest. Before the widespread introduction of fossil fuels in the 1950s, planting of *P. densiflora* accelerated owing to

an increasing demand for fuelwood. The traditional management of this forest continued until almost the end of the 1960s. The second turning point was the fuel revolution that began towards the end of 1950s and the subsequent rapid economic growth in the 1960s and 1970s. Large portions of the former open managed *P. densiflora* forest disappeared
5 as a result of urbanization, conversion into modern agricultural land, and the establishment of dense coniferous plantations of *Cryptomeria japonica* and *Chamaecyparis obtusa* to produce commercial timber. The areas of open *P. densiflora* forest that escaped this land-use conversion were greatly damaged by an outbreak of the pinewood nematode that began towards the end of the 1970s and were abandoned to
10 undergo succession to mixed or deciduous forest (Inui, 1992). Currently, three types of forest (coniferous plantations, mixed forests that developed after the plantations were abandoned, and abandoned deciduous forests) remain in the highly fragmented landscape. Annual management of roadsides along these remnant forests by cutting back the vegetation is conducted both publicly and privately.

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Land-use data

On the basis of the social background of this region, to characterize the pattern of change we selected four time periods (the 1880s, 1950s, 1970s, and 1990s) before and after the major land-use changes described in the previous section. Japan's national map

system is based on a 1-km² grid covering the whole country (Kato et al., 1997). The Geographical Survey Institute of Japan provided a 100×100 m grid of land-use data (each 1-km² cell was subdivided into 100×100-m subcells), with data provided at time intervals of around 5 years from 1974 to 1997. A total of 61 001 of the 100×100-m cells covered the entire study area (Fig. 1). We used the 1974 and 1997 land-use data to represent the 1970s and 1990s periods, respectively. To obtain land-use data for the 1880s and 1950s, we used 1:20 000 scale “quick survey maps” called *jinsoku-sokuzu* and 1:50 000 scale topographic maps, respectively. *Jinsoku-sokuzu* are the oldest Japanese maps created by modern survey methods (plane-table surveys) during the 1880s. The maps are rendered in different colors for forests and grassland or shrubland so that the boundary of each land use is easy to recognize (see Ichikawa et al., 2006). To determine the land-use patterns in the 1950s we used 1:50 000 topographic maps that were created after World War II (from 1952 to 1953). The vector data for the 100×100-m grid covering the study area were overlaid on these old maps in the Mapinfo Professional Version 9.2 GIS (MapInfo Corporation), and the dominant forms of land use were identified for each cell in the grid.

Data collection

We selected 49 cells (each 1 km²) in which agricultural land uses were still dominant in

the 1990s (the cells with dark borders in Fig. 1). Of these cells, 34 had been dominated in the 1880s by forest, 10 by grassland, and 5 by cropland. From July to August 2007, we surveyed the full area within each cell and sampled the roadside vegetation along the forests at one to three randomly selected sample sites per cell. All of these sample sites were located within different 100×100-m cells, and the total was 91 sample sites. The occurrence of all herbaceous, grass, and woody species was recorded along the roads within 1 to 2 m from the pavement edge. The cover values of these species were also estimated by the methods of Braun-Blanquet (Braun-Blanquet, 1964). The total length of road surveyed at each site ranged from 12 to 48 m, depending on the length of the forest edge. We also recorded the forest type (broadleaved, coniferous, or mixed), edge direction (eight compass directions), road width (unpaved < 3 m, and paved < 3 m, 3 to 5.5 m, and > 5.5 m), land use at the opposite side of the road (cropland, forest, or other), and steepness (flat or sloping), and used this data as parameters to describe current site conditions.

To identify the land-use pattern at each sampled site (focusing on the history of cultivation), we analyzed the land-use sequence for each 100×100-m cell that contained our survey sites. To determine whether there were any traces of cultivation during the intervening periods, we also examined aerial photographs taken in 1954, 1964, 1974, and 1990. On the basis of this analysis, we classified the 100×100-m cells (including 91

sampled sites) into three groups: LU_NC, cells with no history of cultivation (50 sites); LU_CL1880, cells cultivated only in the 1880s and with no history of modern agriculture (15 sites); and LU_CL1950, cells cultivated after the 1950s and thus representing the period of modern agriculture (26 sites). In this context, “modern
5 agriculture” represents deep plowing combined with chemical fertilization.

To evaluate the historical impacts of the landscape structure around the sample sites, we focused on the relative abundance of suitable habitats (i.e., ones capable of sustaining grassland vegetation) at different spatial scales around the sites. We considered both forested and grassland cells (including the wasteland land-use type that
10 has developed in recent years, and that is represented by the same symbol as is used for past grassland) as equally suitable habitats, because the species composition in the understory of well-managed open secondary forest was similar to that of semi-natural grassland until at least the end of the 1960s (Fujii and Zinnai, 1979; Yamamoto and Itoga, 1988). We used land-use data for the 100×100-m cells for each of the four time
15 periods, and we calculated the proportions of grassland and forest cells surrounding the central cell that contained the sampled site. The proportions of suitable (grassland and forest) cells were calculated at five different spatial scales (3×3, 5×5, 7×7, 11×11, and 15×15 cells) and used as indices of the proportion of suitable habitat around each sample site. To perform this analysis, we used version 8.5 of the ERDAS IMAGINE

software (ERDAS, 2001).

Data analysis

The analyses consisted of three steps. First, we assessed the relationships between
5 forest-edge vegetation and the present site conditions and past land use. Second, we
evaluated the effects of the proportion of suitable habitat around sites on the present
grassland species richness at different temporal and spatial scales within each of the
three land-use categories. Finally, we evaluated the relative importance of the past and
present impacts of habitat conditions and surrounding areas on the present grassland
10 species richness.

The species compositions of the forest-edge vegetation were described by
using Shannon's H' , which is defined as:

$$H' = - \sum_{i=1}^n (p_i \log p_i) \quad (1)$$

where p_i is the relative abundance of species i on the basis of its cover value,
15 and n is the number of species recorded at the site. The richness values for all species
and for several different species groups (grassland species, other native perennials,
native annuals, exotic species, and woody species) were also calculated. We used the
generalized linear model (GLM) to assess the relationship between these measures of
species diversity and richness and the present site conditions. The effects of the spatial

autocorrelation among sites were also tested by using the set of coordinates calculated using the GIS software as explanatory parameters of the GLM model. All the models used a logarithmic link function that followed a Poisson distribution, except for Shannon's H' , which followed a Gaussian distribution. To investigate the impact of past
5 land-use on the present grassland species richness, we used two nonparametric statistical methods (the Kruskal-Wallis test and Bonferroni's multiple-comparison test) to identify significant differences in the average richness of grassland species between the land-use categories.

To identify the relationships between the present grassland species richness and
10 the values of the proportion of suitable habitat since the 1880s within each land-use category, we derived GLM models using a logarithmic link function that followed a Poisson distribution. In each land-use category, we tested one-on-one relationships between the richness of grassland species and the proportional values of grassland, forest and total (grassland + forest) suitable habitat for the four time periods and the five
15 spatial scales. The additive effects of the proportion of total suitable habitat in different time periods were also estimated within each spatial scale. Then, to compare the evidence in support of proposed models for each land-use category, we used Akaike's information criterion (AIC). We calculated ΔAIC to express the difference between each model and the model with the best fit (i.e., the one with the lowest AIC value) within

each land-use category. AIC differences of between 0 and 2 indicate substantial support for a model, whereas differences greater than 4 indicate low or no support for the model (Burnham and Anderson, 2002).

Finally, in order to compare the relative impacts of the present habitat conditions and of the past land-use and proportions of suitable habitat on the present grassland species richness, we used the GLM procedure and model selection based on both AICc (Akaike's information criterion adjusted for small sample sizes) and the AICc differences (i.e., $\Delta AICc$). In this procedure, all the significant past and present explanatory parameters identified in the former analyses were included. In order to identify the relative importance of the past and present explanatory parameters, We calculated the Akaike weight (w_i) of each plausible model as an indicator of the strength of evidence that the selected best model is convincingly the best; w_i ranges from 0 to 1 and provides an effective way to scale and interpret the Δ_i (Burnham & Anderson, 2002). The sum of Akaike weights of models that include a particular parameter can be used as weight of evidence of the importance of that parameter. We also calculated VIF values of each explanatory parameter included in the model in order to identify the effect of multicollinearity. All the statistical procedures were performed with R software (version 2.4.1; R Development Core Team, 2006).

Results

We recorded a total of 278 species at the 91 sample sites, including 37 typical grassland species (Appendix A). The vegetation compositions in the different land-use patterns are shown in the Supplementary data. Almost 35% of the total species were found in only one of the three land-use patterns, with 67 species restricted to LU_NC sites, 18 species to LU_CL1880 sites, and 10 species to LU_CL1950 sites. A total of 112 species could be found in all groups. The average total lengths of the sampled forest-edge vegetation did not differ significantly among these groups (Table 1).

Shannon's H' did not differ significantly between the three land-use patterns, but the richness values for all species, grassland species, and woody species were significantly lower in LU_CL1950 than the other land-use patterns; none of the richness values differed between LU_NC and LU_CL1880 (Table 1). The grassland species richness was also correlated with the present habitat conditions, the forest type (d.f. = 2, $p < 0.001$), edge direction (d.f. = 7, $p = 0.020$), road width (d.f. = 3, $p = 0.024$), and steepness (d.f. = 1, $p = 0.026$). The richness values of exotic species, native annuals, and native perennials (excluding grassland species) did not differ significantly between land-use patterns but were significantly correlated with the present site conditions. The species richness values for exotic species and native annuals were correlated with edge direction (d.f. = 7, $p = 0.003$ and $p < 0.001$, respectively) and with road width (d.f. = 3,

$p = 0.010$ and $p < 0.001$, respectively). The land-use on the opposite side of the road also influenced the richness of exotic species (d.f. = 2, $p = 0.005$). The richness value for native perennials (excluding grassland species) was correlated with the present forest type (d.f. = 2, $p = 0.014$) and with edge direction (d.f. = 7, $p = 0.006$). There were
5 no significant spatial autocorrelation effects among the sites.

The average proportion of grassland differed significantly between the three land-use patterns in the 1880s, whereas the proportion of forest differed significantly at smaller spatial scales in the 1950s and 1970s (Table 2a). The average proportion of total suitable habitat became similar between groups in the 1970s and 1990s. In LU_NC,
10 significant positive effects of the proportions of grassland, forest and total suitable habitat around sample sites on the present grassland species richness appeared at various spatial scales (Table 2b). The best-fit model (the one with the smallest AIC score) among the resulting 60 models was significantly correlated with the proportion of total suitable habitat in the 1950s at a 5×5 grid scale. All the other models with significant
15 values, except for the model that include forest proportion at a 5×5 grid scale in the 1950s, had ΔAIC values greater than 4, and thus had low, or no explanatory power compared with the best-fit model. In LU_CL1880, no positive effects of the proportions of grassland, forest and total suitable habitat around sample sites were evident, although the proportions of forest and total suitable habitat at a 15×15 grid scale in the 1970s

showed slight negative effects on the present grassland species richness. In LU_CL1950, the grassland proportion at a 15×15 grid scale in the 1990s had a negative effect on the present species richness, and the forest proportion at a 15×15 grid scale in the 1880s had a slight positive effect on the present grassland species richness. Additive effects of the proportion of total suitable habitat on the present grassland species richness could also be recognized at 5×5 and 7×7 spatial scales in LU_NC (Table 3). The best-fit model (with the smallest AIC score) included the proportion of total suitable habitat in the 1950s, 1970s, and 1990s at a 5×5 spatial scale. The proportions of total suitable habitat in the 1950s and 1970s showed significant positive effects on the present grassland species richness, whereas that in the 1990s showed a significant negative effect.

Finally, the model selection procedure that included all the significant past and present explanatory parameters suggested that twelve models could be considered as plausible (i.e., $\Delta AICc < 4$; Table 4). The full model included four types of present variables (forest type, edge direction, road width and steepness), and the five past variables (land-use pattern and the proportions of total suitable habitat in the 1880s, 1950s, 1970s, and 1990s at a 5×5 grid scale). VIF values of all these explanatory parameters were smaller than 5. The land-use pattern and the present forest type, road width, and steepness showed significant relationships with the present grassland species richness. The importance values of all these factors within the plausible models were 1,

while those of the proportions of total suitable habitat in the 1880s, 1950s, 1970s and 1990s at a 5×5 spatial scale were 0.384, 0.463, 0.769, 0.342, respectively.

Discussion

5 Even in highly disturbed forest-edge vegetation along roads, the impacts of historical land-use at a site and of the surrounding areas on the present distribution of semi-natural grassland species could be recognized. This information is thus useful not only for explaining present diversity patterns of grassland species but also for targeting sites for future restoration among remnant abandoned or planted forests to enhance grassland
10 species diversity in the *satoyama* landscape.

Impacts of land-use history on sites

In the present forest-edge vegetation along roads, the appearance of exotic and annual species was influenced only by the present site conditions, whereas the diversity pattern
15 of grassland species showed distinct relationships with not only the present site conditions but also the historical land-use pattern. Grassland species richness in LU_CL1950 (cells cultivated since the 1950s) was much lower than that in LU_NC (uncultivated cells), whereas average grassland species richness in LU_CL1880 (cells cultivated in the 1880s) was not significantly different from that in LU_NC (Table 1).

This suggests that habitat suitability had recovered and that some of the grassland species had recolonized sites classified as LU_CL1880 but not sites classified as LU_CL1950 after the cessation of cultivation. Whether the roadside itself was ever cultivated is unclear, but linear habitats such as the forest-edge vegetation might have
5 been affected directly by the cultivation history of the adjacent forested sites. Although we conducted no physicochemical surveys of soil properties, unfavorable conditions (with respect to eutrophication and acidification) at LU_CL1950 sites might persist as a result of the major abiotic constraints imposed by modern farming practices that use large amounts of fertilizer and pesticides (Verheyen et al., 2003; Falkengren-Grerup et
10 al., 2006; Johansson et al., 2008). At the sites classified as LU_CL1880, such constraints might no longer exist because of a lack of the intensified impacts associated with modern agriculture when the sites were cultivated more than 100 years ago. Moreover, sites formerly cultivated in the 1880s had been replanted and managed as open secondary forest until almost the end of the 1960s (Sakiyama and Itoga, 1994).
15 Continuity of regular management after the cessation of cultivation or abandonment can have positive effects such as the improvement of habitat quality for semi-natural grassland species (Cousins and Eriksson, 2001, 2002; Johansson et al., 2008). Regular management after the cessation of cultivation for more than 50 years also seems to have contributed to the present grassland species diversity in this region.

Different effects of the proportion of suitable habitat around sites with different land-use histories

The past proportions of suitable habitat in areas surrounding the sample sites
5 had different effects on the present diversity of grassland species in the forest-edge
vegetation for sites with different land-use history. Although the average grassland
species richness did not differ significantly between LU_NC and LU_CL1880 (Table 1),
positive effects of the proportion of suitable habitat were apparent in LU_NC, but not in
LU_CL1880 (Table 2b). This result suggested that the land-use history of a site affected
10 the relative importance of the proportion of suitable habitat around the site during the
past 100 years.

In LU_NC, the present grassland species richness and the proportions of forest
and total (grassland + forest) suitable habitat in the 1950s were significantly correlated
at a 5×5 grid scale. This result suggests that the present-day variation in grassland
15 species composition in forest-edge vegetation along roads is a legacy of changes that
began more than 50 years ago. The diversity of grassland species is more strongly
correlated with the past than with the present habitat connectivity because of the
time-lags exhibited by populations of long-lived perennials after landscape changes
(Lindborg and Eriksson, 2004; Cousins et al., 2007). The best-fit model of the additive

effects at different time periods showed that the present grassland species richness was strongly and positively correlated with the proportion of total suitable habitat in the 1950s and 1970s, but negatively correlated with that in recent years (the 1990s). In LU_NC, most of the sites had been surrounded by grassland or forest during the 1880s (about 70% to 90% at all spatial scales), but the grassland proportion decreased drastically (to 0% to 1%) in the 1950s, with only the open secondary forest remaining as suitable habitat for grassland species. The former grassland area had gradually been converted into cultivated land during this period as a result of the agrarian land reforms that occurred in Japan after World War II. Examination of the social background in this region suggests that the drastic decrease in habitats for grassland species (i.e., managed open forest) accelerated after the 1970s (Sakiyama and Itoga, 1994), but the landscape structure before the 1950s might have already formed the present-day diversity patterns of the grassland species.

The lack of any significant difference between the present grassland species richness in LU_NC and LU_CL1880 suggested that some of the grassland species had recolonized the sites in LU_CL1880 after the cessation of cultivation. However, we found no significant positive effects of the proportion of suitable habitat on the present grassland species richness in any time period or at any spatial scale in LU_CL1880 (Table 2b). The negative effect of proportions of forest and total suitable habitat

observed at a 15×15 scale in the 1970s was slightly significant. In the 1970s and 1990s, the average proportions of suitable habitat had already become quite low, and a large portion of the potentially suitable habitats had disappeared as a result of abandonment of the land and rapid urbanization (Sakiyama and Itoga, 1994). Before the agrarian land reforms in the 1950s, shifting agriculture was practiced in this region. Local history literature has described this practice as short-term cultivation and subsequent replanting of *P. densiflora* (Inui, 1992). These areas of short-term cultivation were closely surrounded by traditionally managed open forests, which contained an abundant pool of grassland species. Cousins and Lindborg (2008) showed a clear trend of stepwise dispersal of grassland species from source populations into restored sites over a distance of less than 20 m. In our study area, the abundant actual pool of grassland species in adjacent areas and regular management after the cessation of cultivation until almost the end of the 1960s may have contributed to recolonization of the former arable land in the 1880s. We could not negate the potential effect of low sample size in LU_1880 (15 sites) on the lack of significant effects of the past proportion of suitable habitat, however, the past habitat condition at a grid scale of less than 100×100 m (i.e., with the existence of an immediately adjacent seed source) might have affected the recovery process of the grassland species and might thus have affected the present species distribution in sites that have lost their former populations of grassland species to cultivation.

In LU_CL1950, the average grassland species richness was low (Table 1) and there were no significant effects of the proportions of grassland and total suitable habitat on grassland species richness in any time period or at any spatial scale (Table 2b). The modern cultivation practices used since the 1950s would have imposed major abiotic constraints on the grassland species (Walker et al., 2004), thus negating any positive effects of the proportion of suitable habitat around the sites. Moreover, in a landscape as highly fragmented as the one that has developed since the 1970s, the lack of source populations around sites could prevent recolonization by grassland species even after recovery of the habitat's suitability for grassland species (Cramer et al., 2008). The significant negative effect of the grassland proportion in the 1990s might represent the negative impacts of urban development in the surrounding area on the present grassland species. The traditional grassland cells had totally disappeared by the 1950s, and most of the grassland cells in the 1990s included the land with open vegetation reclaimed for further development, which is expressed using the same land-use pattern on maps (Japan Map Center, 2005). The recent urbanization might also negatively affect the present grassland species richness.

Positive effects of the past proportion of suitable habitat were detected only at 5×5 and 7×7 grid scales (i.e., within 700-m squares) in LU_NC, and they were not apparent at grid scales of more than 1 km (Table 2b, 3). Although we could not compare

our results directly with previous studies (e.g. Lindborg and Eriksson, 2004) because of differences in the connectivity measurements, the effective spatial scales (within 5×5 or 7×7 grid scales, which is comparable to radii of 250- and 350 m) in our study were quite smaller than that (almost 1-km radius) in the previous study. There may be two reasons
5 for this difference. One is the effects of the land-use allocation pattern in our region's traditional landscape. In our study area, the traditional interval between settlements averaged 0.5 to 1 km (Yamaoka et al., 1977), and the semi-natural grassland and forest comprised large proportions of the central plateau at almost the same distance from each village. The traditional land-use allocations and agricultural practices might be
10 responsible for the dispersal of species within the landscape, which was repeated to occur at 0.5- to 1-km diameter or square scales (which is comparable to 5×5 or 7×7 grid scale) in this region, and this would have affected grassland species distribution both in the past and in the present (Poschlod and Bonn, 1998; Lindborg and Eriksson, 2004).

A difference in the measurements might also be responsible for the different
15 spatial effects. We used a simple method in which we summed the proportional areas of potentially suitable habitats (grid cells) in the landscape, and we did not consider the spatial structure of those cells (i.e., the areas or shapes of connected cells and their distances from the central cell). Most previous studies used Hanski's connectivity measure, which defines connectivity as the sum of areas with suitable habitat, weighted

by their distance from the target site (Hanski, 1999). To account for the effects of surrounding landscape structure more precisely, we should consider both habitat attributes and their spatial configuration within the landscape, because these factors have a relatively large effect on dispersal of plant species (Moilanen and Nieminen, 5 2002). When these complex connectivity measures are considered, however, the feasibility of data acquisition and parameter estimation should be a central consideration (Moilanen and Nieminen, 2002). Although we did not include the effective factors in our simple measurement, we were nonetheless able to estimate the effects of past and present land-use by using grid-based national-scale land-use data. This makes our 10 approach especially useful at larger spatial scales.

Conservation implications of historical information

Our model-selection procedure showed that the land-use pattern at a site was one of the most important factors for explaining the present distribution of grassland 15 species (Table 4). All the twelve plausible models also included the total proportion of suitable habitat around a site in the past, especially in the 1970s at a 5×5 spatial scale. This result emphasizes the necessity to focus on both the land-use history of a site and on the surrounding landscape structure for better explanation of the present distribution of grassland species even in remnant linear habitats within highly fragmented

agricultural landscapes. The negative impacts of present habitat conditions, combined with the past impacts of cultivation and habitat fragmentation in the surrounding area for more than 50 years, might adversely affect remnant populations of grassland species, leading to further loss of species diversity. The forest-edge vegetation along roads will

5 be guaranteed to have continuity of management, because this management is required for vehicle safety, and this might have positive effects on flowering and seed production of grassland species (Jantunen et al., 2007). Resuming extensive management of the abandoned or planted forests that retain a pool of some grassland species in the roadside vegetation could enable such seed sources to recolonize the forest sites, thereby

10 enhancing grassland species diversity. Information on the historical pattern of local site conditions and on the scale of the matrices within which these patterns exert their influence can provide useful explanations of present diversity patterns. This information can also help managers to target sites for future restoration among abandoned or planted forests that remain potentially suitable habitats for grassland species within the highly

15 fragmented modern *satoyama* landscape.

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Appendix

List of the 37 grassland species found at the 91 study sites. The number (and %) of sites was recorded for three groups with different land-use patterns (LU_NC = uncultivated sites, LU_CL1880 = sites cultivated in the 1880s, LU_CL1950 = sites cultivated after the 1950s).

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	Life form	Dispersal type	Flowering season start	Flowering season duration	All (n=91) (%)	LU_NC (n=50) (%)	LU_CL1880 (n=15) (%)	LU_CL1950 (n=26) (%)
<i>Rubus parvifolius</i>	Ch	D ₂	spring	medium	43 (47.3)	33 (66.0)	6 (40.0)	4 (15.4)
<i>Miscanthus sinensis</i>	H	D ₁	late summer	medium	38 (41.8)	25 (50.0)	6 (40.0)	7 (26.9)
<i>Smilax china</i>	N	D ₂	spring	medium	34 (37.4)	27 (54.0)	5 (33.3)	2 (7.7)
<i>Desmodium podocarpium</i> ssp. <i>oxyphyllum</i>	H	D ₂	early summer	long	26 (28.6)	19 (38.0)	2 (13.3)	5 (19.2)
<i>Polygonatum odoratum</i> var. <i>pluriflorum</i>	G	D ₂	spring	short	23 (25.3)	18 (36.0)	2 (13.3)	3 (11.5)
<i>Viola grypoceras</i>	H	D ₃	spring	short	19 (20.9)	13 (26.0)	6 (40.0)	0 (0.0)
<i>Lespedeza pilosa</i>	H	D ₄	early summer	medium	18 (19.8)	13 (26.0)	4 (26.7)	1 (3.8)
<i>Albizia julibrissin</i>	M	D ₁	early summer	short	15 (17.6)	11 (22.0)	2 (13.3)	2 (7.7)
<i>Imperata cylindrica</i> var. <i>koenigii</i>	G	D ₁	spring	short	15 (16.5)	9 (18.0)	2 (13.3)	4 (15.4)
<i>Lespedeza bicolor</i>	N	D ₄	early summer	long	15 (16.5)	14 (28.0)	1 (6.7)	0 (0.0)
<i>Sanguisorba officinalis</i>	H	D ₄	early summer	medium	15 (16.5)	14 (28.0)	1 (6.7)	0 (0.0)
<i>Potentilla freyniana</i>	H	D ₄	spring	medium	14 (15.4)	12 (24.0)	1 (6.7)	1 (3.8)
<i>Pteridium aquilinum</i> var. <i>latiusculum</i>	G	D ₁	-	-	14 (15.4)	12 (24.0)	1 (6.7)	1 (3.8)
<i>Thalictrum minus</i> var. <i>hypoleucum</i>	H	D ₄	early summer	medium	13 (14.3)	12 (24.0)	1 (6.7)	0 (0.0)
<i>Potentilla fragarioides</i> var. <i>major</i>	H	D ₄	spring	medium	13 (14.3)	11 (22.0)	1 (6.7)	1 (3.8)
<i>Carex lanceolata</i>	H	D ₄	spring	medium	13 (14.3)	5 (10.0)	7 (46.7)	1 (3.8)
<i>Hydrocotyle ramiflora</i>	Ch	D ₄	early summer	long	11 (12.1)	8 (16.0)	1 (6.7)	2 (7.7)
<i>Ixeris dentata</i>	H	D ₁	spring	medium	10 (11.0)	8 (16.0)	2 (13.3)	0 (0.0)
<i>Cirsium oligophyllum</i>	H	D ₁	late summer	medium	10 (11.0)	9 (18.0)	1 (6.7)	0 (0.0)
<i>Lysimachia clethroides</i>	H	D ₄	early summer	short	7 (7.7)	5 (10.0)	2 (13.3)	0 (0.0)
<i>Agrimonia japonica</i>	H	D ₂	early summer	long	7 (7.7)	4 (8.0)	2 (13.3)	1 (3.8)
<i>Calamagrostis arundinacea</i> var. <i>brachytricha</i>	H	D ₁	late summer	medium	7 (7.7)	5 (10.0)	1 (6.7)	1 (3.8)
<i>Eupatorium chinense</i> var. <i>oppositifolium</i>	H	D ₁	late summer	medium	7 (7.7)	3 (6.0)	4 (26.7)	0 (0.0)
<i>Cirsium japonicum</i>	H	D ₁	early summer	medium	6 (6.6)	6 (12.0)	0 (0.0)	0 (0.0)
<i>Liriope minor</i>	H	D ₂	early summer	long	6 (6.6)	5 (10.0)	0 (0.0)	1 (3.8)
<i>Picris hieracioides</i> var. <i>glabrescens</i>	Th	D ₁	spring	long	4 (4.4)	2 (4.0)	0 (0.0)	2 (7.7)
<i>Aster scaber</i>	H	D ₁	late summer	medium	3 (3.3)	3 (6.0)	0 (0.0)	0 (0.0)
<i>Euphorbia pekinensis</i>	H	D ₃	early summer	short	3 (3.3)	2 (4.0)	1 (6.7)	0 (0.0)
<i>Adenophora triphylla</i> var. <i>japonica</i>	H	D ₄	late summer	medium	3 (3.3)	3 (6.0)	0 (0.0)	0 (0.0)
<i>Hypericum erectum</i>	H	D ₁	early summer	short	2 (2.2)	2 (4.0)	0 (0.0)	0 (0.0)
<i>Indigofera pseudotinctoria</i>	N	D ₄	early summer	long	2 (2.2)	2 (4.0)	0 (0.0)	0 (0.0)
<i>Solidago virgaurea</i> var. <i>asiatica</i>	H	D ₁	late summer	medium	1 (1.1)	1 (2.0)	0 (0.0)	0 (0.0)
<i>Ixeris debilis</i>	H	D ₁	spring	short	1 (1.1)	1 (2.0)	0 (0.0)	0 (0.0)
<i>Artemisia japonica</i>	H	D ₄	late summer	long	1 (1.1)	1 (2.0)	0 (0.0)	0 (0.0)
<i>Zoysia japonica</i>	G	D ₄	spring	short	1 (1.1)	1 (2.0)	0 (0.0)	0 (0.0)
<i>Viola verecunda</i>	H	D ₃	spring	short	1 (1.1)	1 (2.0)	0 (0.0)	0 (0.0)
<i>Lespedeza cuneata</i>	H	D ₄	late summer	medium	1 (1.1)	0 (0.0)	0 (0.0)	1 (3.8)

Life form: Th = therophyte, G = geophyte, H = hemicryptophyte, Ch = chamaephyte, N = nanophanerophyte, and M = Microphanerophyte. Dispersal type: D₁ = anemochorous, D₂ = zoochorous, D₃ = autochorous, and D₄ = bolochorous. Month of flowering start: spring = from March to May; early summer = from June to July; and late summer = from August. Duration of the flowering periods: short = less than 2 months, medium = 3 or 4 months, long = more than 5 months.

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Table 1 Total lengths of the sampled roadside vegetation, species diversity (Shannon's H'), and species richness in the three different land-use patterns (LU_NC = cells with uncultivated sites, LU_CL1880 = cells with cultivated sites in the 1880s, LU_CL1950 = cells with cultivated sites after the 1950s). Differences were tested for significance by nonparametric statistical methods (the Kruskal-Wallis test and Bonferroni's multiple-comparison test). Values in a row followed by different letters differ significantly ($p < 0.05$).

	LU_NC ($n = 50$)		LU_CL1880 ($n = 15$)		LU_CL1950 ($n = 26$)	
	Avg	(SD)	Avg	(SD)	Avg	(SD)
Total length (m)	29.7	(10.2)	26.2	(12.7)	24.0	(7.7)
Shannon's H'	2.43	(0.37)	2.43	(0.40)	2.26	(0.46)
<i>Species richness</i>						
All species	37.02	(10.10) ^a	37.87	(10.20) ^a	28.73	(7.20) ^b
Grassland species	4.02	(3.35) ^a	2.73	(2.22) ^a	1.15	(1.32) ^b
Exotic species	2.94	(1.88)	3.20	(2.54)	3.04	(2.44)
Native annuals	5.14	(3.31)	6.07	(4.98)	6.31	(4.84)
Native perennials	12.72	(4.46)	13.07	(4.56)	11.50	(4.16)
Woody species	14.54	(5.41) ^a	15.33	(4.43) ^a	9.12	(4.88) ^b

Table 2. (a) Average proportions of suitable habitat (i.e., the proportion of the cells adjacent to a sample site that are suitable for grassland species) for each time period and spatial scale for the three different land-use patterns (LU_NC = cells with uncultivated sites, LU_CL1880 = cells with cultivated sites in the 1880s, LU_CL1950 = cells with cultivated sites after the 1950s). Grid cells are each 100×100 m. Nonparametric statistical methods (the Kruskal-Wallis test and Bonferroni's multiple-comparison test) were used to test for significant differences. Values within a row followed by different letters differ significantly ($p < 0.05$). (b) GLM models for the changes in grassland species richness as a function of the proportion of suitable habitat for each time period and spatial scale, using a logarithmic link function that followed a Poisson distribution within each land-use category. Differences in Akaike's information criterion (ΔAIC) show the difference between each value and the value for the model with the best fit ($\Delta AIC = 0$) within each land-use category. Models with $\Delta AIC > 4$ have low or no support; values < 2 have strong support. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

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			(a) Average proportions of suitable habitat			(b) Positive effects of proportions of suitable habitat on the present grassland species richness								
			LU NC (n = 50)	LU CL1880 (n = 15)	LU CL1950 (n = 26)	LU NC			LU 1880s			LU 1950s		
			Avg (SD)	Avg (SD)	Avg (SD)	Estimate	AIC	ΔAIC	Estimate	AIC	ΔAIC	Estimate	AIC	ΔAIC
Grassland														
1880s														
	3×3	0.31 (0.36) _a	0.06 (0.18) _b	0.23 (0.37) _{ab}	-0.345	284.8	19.1	-1.626	66.9	4.4	0.106	82.2	5.8	
	5×5	0.31 (0.34) _a	0.06 (0.17) _b	0.21 (0.35) _{ab}	-0.333	285.2	19.6	-1.202	67.7	5.1	0.108	82.2	5.8	
	7×7	0.30 (0.32) _a	0.08 (0.17) _b	0.19 (0.31) _b	-0.360	285.2	19.5	-1.161	67.7	5.1	0.004	82.2	5.9	
	11×11	0.28 (0.29) _a	0.10 (0.18) _b	0.16 (0.27) _{ab}	-0.303	286.2	20.5	-1.140	67.5	4.9	-0.302	82.1	5.7	
	15×15	0.25 (0.26) _a	0.10 (0.16) _b	0.14 (0.24) _b	-0.234	286.9	21.2	-1.458	67.1	4.6	-0.502	81.9	5.5	
1950s														
	3×3	0.00 (-)	0.00 (-)	0.00 (-)	-	-	-	-	-	-	-	-	-	
	5×5	0.00 (0.02)	0.00 (-)	0.00 (-)	6.404***	279.4	13.7	-	-	-	-	-	-	
	7×7	0.00 (0.02)	0.00 (-)	0.00 (-)	6.649**	280.9	15.3	-	-	-	-	-	-	
	11×11	0.00 (0.01)	0.00 (-)	0.00 (0.01)	13.307**	282.0	16.4	-	-	-	-41.540	80.3	3.9	
	15×15	0.00 (0.01)	0.00 (0.00)	0.00 (0.01)	25.089**	281.8	16.2	-74.555	68.5	6.0	-64.633	79.7	3.3	
1970s														
	3×3	0.00 (0.02)	0.00 (-)	0.00 (0.02)	-0.046	287.6	21.9	-	-	-	-1.336	82.2	5.8	
	5×5	0.00 (0.01)	0.00 (0.01)	0.00 (0.01)	-0.127	287.6	21.9	-26.246	67.2	4.7	-3.711	82.2	5.8	
	7×7	0.00 (0.01)	0.00 (0.01)	0.00 (0.01)	5.727	287.2	21.6	-51.441	67.2	4.7	-43.237	81.2	4.9	
	11×11	0.00 (0.00)	0.00 (0.01)	0.00 (0.00)	42.303*	282.7	17.1	-3.094	68.7	6.2	-132.187	78.5	2.1	
	15×15	0.00 (0.00)	0.01 (0.01)	0.00 (0.00)	32.532*	283.5	17.9	-27.480	65.8	3.3	-242.609	77.2	0.8	
1990s														
	3×3	0.02 (0.07)	0.01 (0.04)	0.03 (0.07)	0.467	287.3	21.7	2.622	68.3	5.8	-5.218	80.3	3.9	
	5×5	0.02 (0.05)	0.02 (0.05)	0.03 (0.06)	0.210	287.6	21.9	2.928	67.5	4.9	-7.821	79.5	3.2	
	7×7	0.03 (0.05)	0.02 (0.05)	0.03 (0.06)	1.074	287.0	21.4	2.509	68.0	5.5	-10.514	77.2	0.9	
	11×11	0.02 (0.03)	0.02 (0.04)	0.03 (0.05)	0.968	287.4	21.7	2.742	68.3	5.8	-12.229	77.1	0.7	
	15×15	0.02 (0.02)	0.02 (0.03)	0.03 (0.03)	0.206	287.6	21.9	-0.232	68.8	6.2	-17.456*	76.4	0.0	
Forest														
1880s														
	3×3	0.58 (0.35)	0.42 (0.30)	0.56 (0.37)	0.652**	278.0	12.3	0.102	68.7	6.2	0.686	80.5	4.1	
	5×5	0.56 (0.30)	0.45 (0.26)	0.52 (0.30)	0.733**	279.0	13.3	0.056	68.7	6.2	0.746	80.9	4.5	
	7×7	0.53 (0.26)	0.46 (0.22)	0.53 (0.26)	0.845**	279.1	13.4	-0.641	68.0	5.5	0.976	80.5	4.1	
	11×11	0.47 (0.19)	0.43 (0.17)	0.49 (0.19)	0.603	285.1	19.5	-0.909	67.8	5.3	1.469	80.2	3.8	
	15×15	0.44 (0.15)	0.43 (0.17)	0.47 (0.14)	-0.129	287.5	21.9	-1.211	67.1	4.6	3.219*	77.5	1.2	
1950s														
	3×3	0.67 (0.29) _a	0.39 (0.28) _b	0.59 (0.31) _{ab}	0.922***	274.8	9.1	-1.123	65.6	3.0	-0.360	81.9	5.5	
	5×5	0.65 (0.25) _a	0.44 (0.22) _b	0.58 (0.25) _{ab}	1.345***	267.9	2.2	-1.213	66.3	3.7	0.186	82.2	5.8	
	7×7	0.59 (0.21) _a	0.43 (0.19) _b	0.57 (0.22) _{ab}	1.404***	271.8	6.2	-0.523	68.4	5.8	0.707	81.6	5.2	
	11×11	0.51 (0.16)	0.43 (0.14)	0.52 (0.15)	1.278**	279.5	13.9	-0.793	68.3	5.7	0.715	81.9	5.5	
	15×15	0.47 (0.13)	0.43 (0.11)	0.48 (0.14)	0.866	284.8	19.2	-1.697	67.5	4.9	1.359	81.2	4.8	
1970s														
	3×3	0.56 (0.25) _a	0.42 (0.27) _{ab}	0.40 (0.19) _b	0.508	284.5	18.8	-0.738	67.3	4.8	0.671	81.7	5.4	
	5×5	0.49 (0.19)	0.39 (0.24)	0.40 (0.15)	1.109**	277.9	12.2	-1.246	66.1	3.5	1.119	81.3	4.9	
	7×7	0.42 (0.16)	0.38 (0.20)	0.36 (0.13)	1.390**	277.7	12.0	-1.114	67.2	4.7	0.491	82.1	5.7	
	11×11	0.36 (0.10)	0.35 (0.14)	0.35 (0.13)	1.226	284.5	18.9	-2.196	66.0	3.4	-0.247	82.2	5.8	
	15×15	0.34 (0.08)	0.35 (0.11)	0.32 (0.11)	0.231	287.5	21.9	-3.819*	63.6	1.0	0.408	82.2	5.8	
1990s														
	3×3	0.43 (0.25)	0.36 (0.18)	0.38 (0.20)	0.147	287.3	21.7	0.497	68.4	5.9	0.585	81.8	5.5	
	5×5	0.37 (0.20)	0.30 (0.15)	0.32 (0.14)	0.565	284.8	19.1	0.586	68.4	5.9	0.787	81.9	5.5	
	7×7	0.31 (0.16)	0.30 (0.11)	0.29 (0.11)	0.523	286.2	20.5	0.705	68.5	6.0	-0.157	82.2	5.9	
	11×11	0.26 (0.09)	0.28 (0.08)	0.27 (0.09)	0.343	287.4	21.7	-0.672	68.6	6.1	-0.079	82.2	5.9	
	15×15	0.24 (0.07)	0.27 (0.07)	0.24 (0.08)	-0.325	287.5	21.8	-4.411	65.7	3.1	-0.175	82.2	5.9	
Total (grassland + forest)														
1880s														
	3×3	0.90 (0.18) _a	0.48 (0.32) _b	0.78 (0.28) _a	1.259**	279.6	14.0	-0.247	68.5	6.0	1.930	77.3	0.9	
	5×5	0.87 (0.17) _a	0.51 (0.29) _c	0.73 (0.24) _b	0.948*	283.1	17.5	-0.260	68.5	6.0	1.613	78.9	2.6	
	7×7	0.83 (0.19) _a	0.54 (0.24) _b	0.72 (0.22) _{ab}	0.552	285.6	20.0	-0.993	66.7	4.1	1.517	79.6	3.2	
	11×11	0.75 (0.19) _a	0.53 (0.21) _b	0.66 (0.20) _{ab}	-0.078	287.5	21.9	-1.362	65.7	3.2	0.770	81.6	5.2	
	15×15	0.70 (0.19) _a	0.53 (0.21) _b	0.62 (0.18) _{ab}	-0.526	285.7	20.1	-1.525	64.9	2.4	0.894	81.5	5.1	
1950s														
	3×3	0.67 (0.29) _a	0.39 (0.28) _b	0.59 (0.31) _{ab}	0.922***	274.8	9.1	-1.123	65.6	3.0	-0.360	81.9	5.5	
	5×5	0.65 (0.25) _a	0.44 (0.22) _b	0.58 (0.25) _{ab}	1.396***	265.7	0.0	-1.213	66.3	3.7	0.186	82.2	5.8	
	7×7	0.60 (0.21) _a	0.43 (0.19) _b	0.57 (0.22) _{ab}	1.485***	269.7	4.0	-0.523	68.4	5.8	0.707	81.6	5.2	
	11×11	0.51 (0.16)	0.43 (0.14)	0.52 (0.15)	1.351**	278.6	12.9	-0.793	68.3	5.7	0.609	82.0	5.6	
	15×15	0.47 (0.13)	0.43 (0.11)	0.48 (0.14)	0.918	284.5	18.8	-1.698	67.5	4.9	1.247	81.4	5.0	
1970s														
	3×3	0.56 (0.25) _a	0.42 (0.27) _{ab}	0.41 (0.19) _b	0.511	284.5	18.8	-0.738	67.3	4.8	0.644	81.8	5.4	
	5×5	0.49 (0.19)	0.39 (0.24)	0.40 (0.15)	1.113**	277.8	12.2	-1.302	65.9	3.3	1.111	81.3	5.0	
	7×7	0.42 (0.16)	0.38 (0.20)	0.37 (0.13)	1.355**	277.8	12.1	-1.167	67.1	4.6	0.433	82.1	5.8	
	11×11	0.36 (0.10)	0.36 (0.13)	0.35 (0.13)	1.260	284.3	18.7	-2.440	65.7	3.1	-0.332	82.2	5.8	
	15×15	0.34 (0.08)	0.35 (0.11)	0.32 (0.11)	0.308	287.4	21.8	-4.244*	62.5	0.0	0.331	82.2	5.8	
1990s														
	3×3	0.45 (0.25)	0.37 (0.19)	0.41 (0.22)	0.185	287.1	21.5	0.589	68.3	5.7	0.193	82.2	5.8	
	5×5	0.39 (0.21)	0.32 (0.17)	0.34 (0.15)	0.560	284.7	19.1	0.840	68.0	5.4	-0.009	82.2	5.9	
	7×7	0.34 (0.16)	0.33 (0.13)	0.32 (0.12)	0.585	285.7	20.1	0.883	68.2	5.7	-1.426	81.3	5.0	
	11×11	0.28 (0.09)	0.30 (0.11)	0.30 (0.09)	0.463	287.2	21.6	-0.028	68.8	6.2	-1.896	81.2	4.9	
	15×15	0.26 (0.07)	0.29 (0.08)	0.26 (0.09)	-0.278	287.5	21.8	-3.126	66.6	4.0	-1.711	81.5	5.2	

Table 3. GLM models for the additive effects of proportion of total (grassland + forest) suitable habitat in the different time periods at each spatial scale on the present grassland species richness in LU_NC (cells with uncultivated sites, $n = 50$), using a logarithmic link function that followed a Poisson distribution. All explanatory parameters in the different time periods were included in the modeling process at each spatial scales (3×3, 5×5, 7×7, 11×11, and 15×15), but only the models in which AIC differences (Δ AIC) with the lowest model were smaller than 4 were selected. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

	Grid scale	Estimate				AIC	Δ AIC	
		Intercept	1880s	1950s	1970s			1990s
	5×5	0.1828	-	1.2419 ^{***}	1.8100 [*]	-1.4426 [*]	263.97	0.00
	5×5	0.4258	-	1.3963 ^{***}	-	-	265.65	1.68
	5×5	0.0526	0.1879	1.2054 ^{***}	1.7546 [*]	-1.3967 [*]	265.83	1.86
	5×5	0.3282	-	1.2313 ^{***}	0.4135	-	266.57	2.60
10	7×7	0.2635	-	1.2100 ^{**}	2.2335 ^{**}	-1.7872 [*]	266.64	2.67
	5×5	0.1264	0.4012	1.3178 ^{***}	-	-	267.01	3.04
	5×5	0.4387	-	1.4306 ^{***}	-	-0.0915	267.58	3.61

Table 4. GLM models for using all the past and present significant explanatory parameters related to the present grassland species richness.

The past variables included land-use pattern (LU; LU_NC = cells with uncultivated sites, LU_CL1880 = cells with cultivated sites in the 1880s, LU_CL1950 = cells with cultivated sites after the 1950s), and the proportion of total (grassland + forest) suitable habitat in the 1880s, 1950s, 1970s and 1990s at a 5×5 grid scale. The variables representing present conditions included forest type (Type; broadleaved, 5 coniferous, or mixed), edge direction (eight compass directions), road width (RW; unpaved < 3 m, and paved < 3 m, 3 to 5.5 m, or > 5.5 m), and steepness (ST; flat or sloping). All these predictors were included in the modeling process, but only the models in which AICc differences ($\Delta AICc$) with the model with the best fit ($\Delta AICc = 0$) were smaller than 4 were selected.

Model	No. of parameters	AICc	$\Delta AICc$	Deviance	Akaike weight
1 GR ~ LU + Type + RW + ST + 1970s	10	384.9	0.00	146.8	0.169
2 GR ~ LU + Type + RW + ST + 1970s + 1990s	11	385.4	0.51	144.7	0.131
3 GR ~ LU + Type + RW + ST + 1880s + 1970s	11	385.5	0.64	144.8	0.123
4 GR ~ LU + Type + RW + ST + 1950s + 1970s	11	385.7	0.83	145.0	0.111
5 GR ~ LU + Type + RW + ST + 1950s	10	385.8	0.96	147.7	0.104
10 6 GR ~ LU + Type + RW + ST + 1880s + 1970s + 1990s	12	386.4	1.50	143.0	0.080
7 GR ~ LU + Type + RW + ST + 1950s + 1970s + 1990s	12	386.6	1.77	143.3	0.070
8 GR ~ LU + Type + RW + ST + 1880s + 1950s	11	386.8	1.98	146.1	0.063
9 GR ~ LU + Type + RW + ST + 1880s + 1950s + 1970s	12	387.1	2.28	143.8	0.054
10 GR ~ LU + Type + RW + ST + 1880s	10	388.1	3.25	150.0	0.033
11 GR ~ LU + Type + RW + ST + 1880s + 1950s + 1970s + 1990s	13	388.3	3.41	142.2	0.031
12 GR ~ LU + Type + RW + ST + 1950s + 1990s	11	388.3	3.48	147.6	0.030

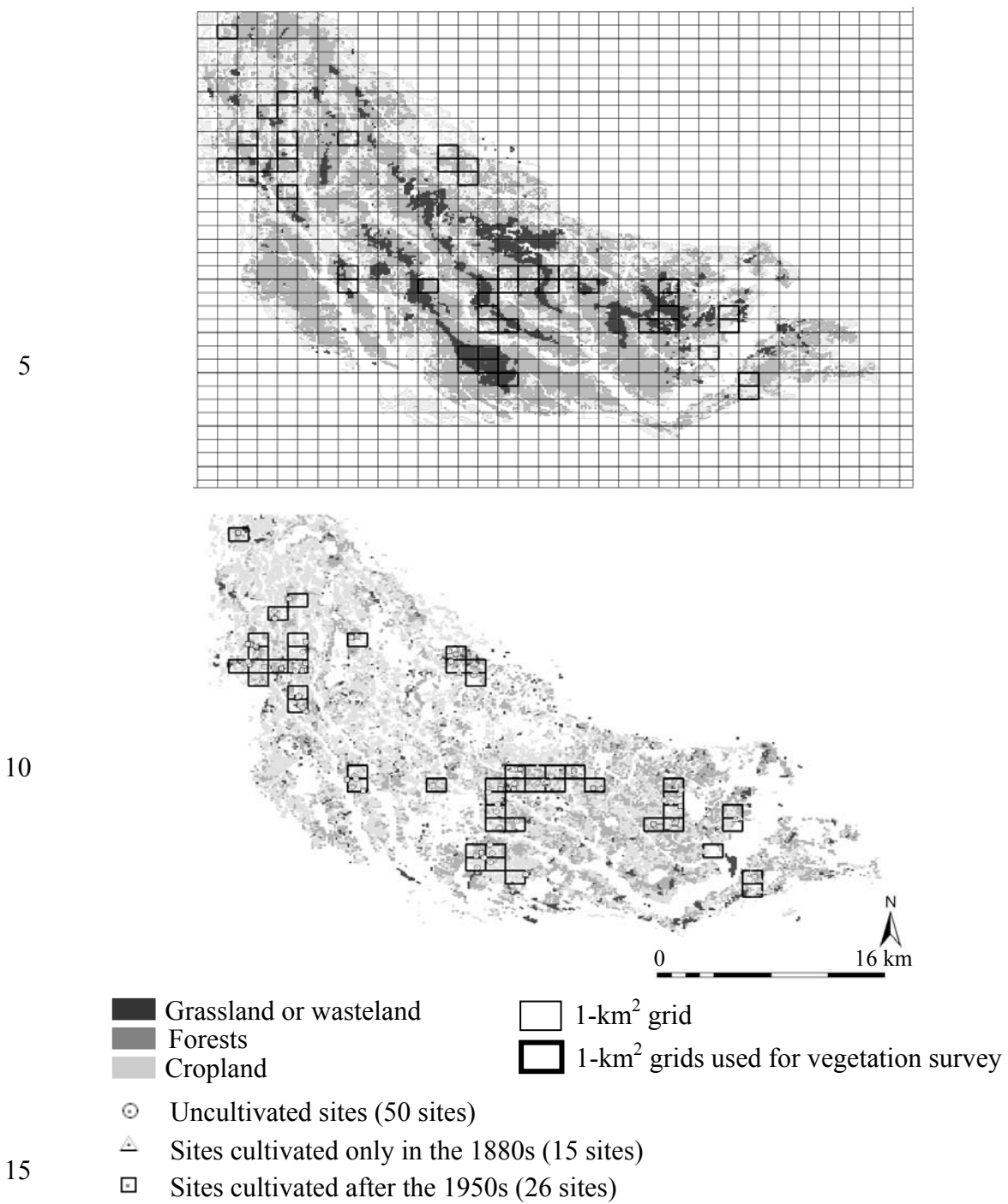


Fig. 1 Land-use data from the 1880s and 1990s were recorded in a 100×100 m grid overlain by 1-km² cells that covered the whole study area. Sites used for the vegetation survey were also shown in the 1990s land-use map according to land-use patterns classified on the basis of cultivation history.