

Millennium-scale changes in mire vegetation reconstructed from plot-based pollen and vegetation analysis and their implications for conservation

Chuh Yonebayashi

Faculty of Geo-Environmental Science, Rissho University, Japan

SUMMARY

Historical perspective helps ecologists and conservationists to better understand modern processes and potential future changes, but collecting long-term ecological data with fine spatiotemporal resolution is challenging. The aim of this study was to reconstruct mire vegetation about 1100 years ago by applying local components that represent the positions of local plants and the mire margin. From the plot-based comparison between modern pollen and vegetation, *Sanguisorba*, other Rosaceae, Ericaceae and *Sphagnum* were considered to be local components that signify the position of source plants within about 1 m. *Ilex*, *Acer* and *Lysichiton* were estimated to have attributes of both local and extra-local components and to indicate the mire margin with a few metres' resolution. These results allowed reconstruction of the millennium-scale changes in the mire's areal extent and local vegetation. The site was a wetter *Sphagnum* mire in 915 CE and has changed to a drier one, with *Geum pentapetalum* now more common. The maximum extent of the mire has retreated about 5 m, although the margin around the depressed northern end has slightly expanded. Nevertheless, the mire has maintained a peatland of similar size during the last millennium. Plot-based pollen and vegetation analysis is useful and can assist ecologists and conservationists to choose the proper conservation procedures.

KEY WORDS: Japan, modern pollen, palynology, peat, tephrochronology

INTRODUCTION

Historical perspective helps ecologists and conservationists to better understand modern processes as well as potential future changes. It can be difficult, however, to collect long-term data with fine spatiotemporal resolution within a reasonable length of time (Yonebayashi 2001). Insights from palaeoecological data can make a significant contribution to biological conservation and habitat management, which are concerned with changes on the order of decades or centuries (Moore *et al.* 1991). Willis & Birks (2006) and Willis *et al.* (2007) highlighted the potential of palaeoecological records, noting that they provide a historical perspective that can help to put present and future conservation and management policies into context. Mire communities and their component species change in response to a variety of factors such as regional climate trends, local hydrology and anthropogenic activities. In order to assess such changes conservation biology and habitat management use records that are based on short-term ecological data (Willis & Birks 2006). It is impossible, however, to know long-term response by use of the short-term data alone. Palaeoecological studies can provide a long-term perspective to address these changes by use of fossil data. While macrofossils are useful for local vegetation

reconstruction, I focused on pollen and spores to develop the palynological methodology in this paper. Much palynological research is focused on reconstructing landscape-scale vegetation history, whereas ecologists and conservationists are primarily interested in local communities.

Sophisticated numerical approaches to the pollen-based reconstruction of past vegetation have been developed (Lindbladh *et al.* 2000, Sugita 2007a, b; Lindbladh & Foster 2010, Sugita *et al.* 2010, Bunting *et al.* 2013, Roberts *et al.* 2018, Li *et al.* 2020). To identify the pollen-source area, vegetation data for these model-based vegetation reconstructions were collected from field surveys and remote-sensing data of various scales. Most of these studies compared the pollen assemblage of a point with many vegetation data from various geographic ranges, which is both time-consuming and laborious (Bunting *et al.* 2013). Moreover, in areas with vegetation in a mosaic, it remains difficult to estimate the relative pollen productivity, which is essential for model-based vegetation reconstruction (Broström *et al.* 2004, 2008).

An indicator approach to distinguishing local elements from regional ones would make it easier to reconstruct local vegetation if the estimations in advance are reliable. I previously proposed local components based on a comparison between modern



pollen assemblages and vegetation from presence/absence data obtained from all plots in a mire and applied them to reconstruct changes in local vegetation and areal extent from 915 CE (Yonebayashi 1996, 2001). Empirical knowledge of such changes in the local vegetation contributes to the conservation and management of mire ecosystems. This method, however, was insufficient because the criteria for estimating local components could have been affected by the number of plots.

The aim of the present study was to reconstruct millennium-scale changes in a mire ecosystem by applying local components that represent the positions of local plants and the mire margin. To select reliable local elements, I compared modern pollen assemblages and local vegetation and then applied a plot-based association index (Davis 1984) on the basis of the pollen and plant coexistence probability. Based on those results, I reconstructed the local vegetation and extent of the mire in 915 CE when vegetation in this area remained virtually intact. The synchronous level of the past surface in 915 CE was determined by a tephra layer.

METHODS

Study site

The Takada-yachi Mire (approximately 170 m × 70 m, elevation above sea level 1027 m) is located in the Hakkoda Mountains of northern Japan (Figure 1;

40° 38.0' N, 140° 52.9' E). The mire is one of several mires situated on a saddle between the northern and southern Hakkoda Mountains (e.g. Sasaki *et al.* 2013). The mire's peat is approximately 200 cm thick, and includes tephra layers (Yamanaka 1963, 1978; Yoshioka 1963). The Towada volcano, which yielded the Towada-a and -b (To-a and To-b) tephras, is located about 15 km to the south. Two tephras, To-a and B-Tm, which are often found in the uppermost part of peat sections on northern Honshu Island, are well preserved in the Takada-yachi peat. The B-Tm tephra is attributed to an eruption of Mount Baegdusan on the border between China and North Korea in 946 CE (Oppenheimer *et al.* 2017), and the To-a tephra is estimated to have fallen in 915 CE (Yonebayashi 1996). I focused on the lower distinct To-a tephra to determine a synchronous level of the peat surface in 915 CE.

The study area is within Towada-Hachimantai National Park and is predominantly forested; hence, natural vegetation is well preserved. According to Yoshioka & Kaneko (1963), the montane deciduous broad-leaved forest zone in this area extends up to 900–1000 m and the subalpine coniferous forest zone lies above this zone. *Pinus pumila* scrub occupies summit areas. On eastern slopes at high elevations (above 1100–1300 m), the forest cover is interrupted by treeless vegetation that grows in areas of late-melting snowdrifts. The montane deciduous broad-leaved forest is dominated by *Fagus crenata*. Species such as *Viburnum furcatum*, *Magnolia salicifolia*,

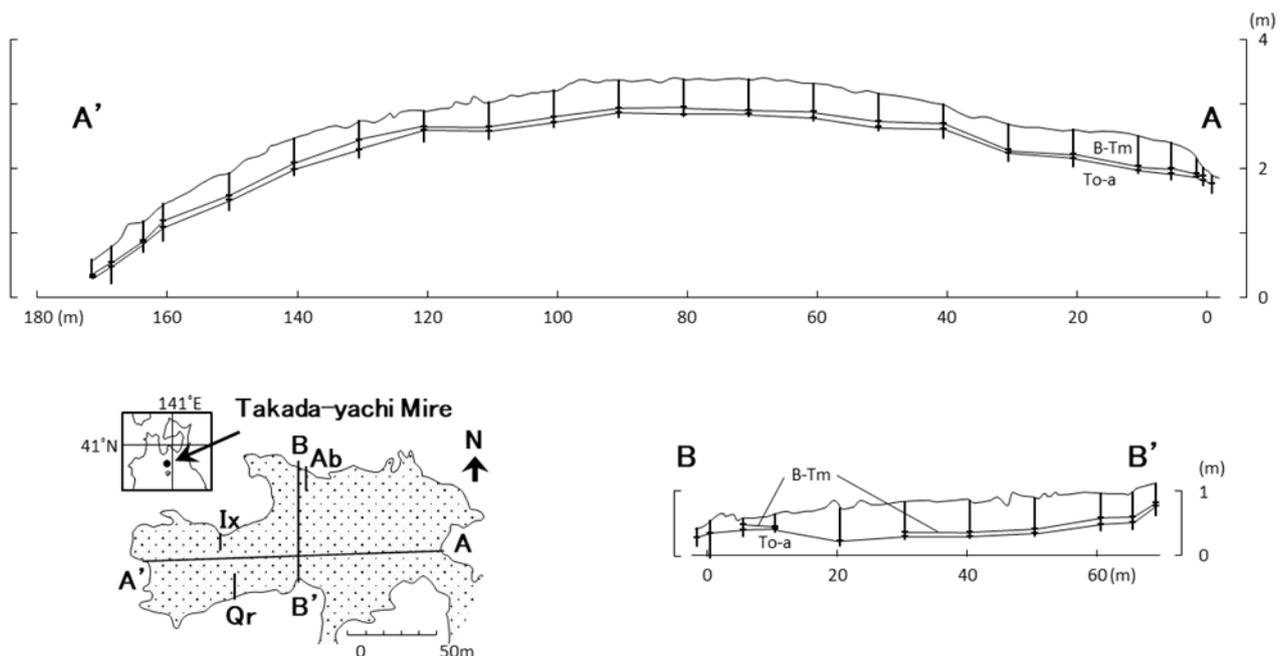


Figure 1. The Takada-yachi Mire, northern Japan, showing the profiles with two tephras (To-a and B-Tm) and the locations of sampling plots along the two major transect lines (Line A and Line B).

Daphniphyllum macropodum subsp. *humile* and *Sasa kurilensis* are common in the understorey. *Abies mariesii* dominates the subalpine coniferous forest zone, with abundant *Betula ermanii*. The *A. mariesii* forest has an understorey comprising *S. kurilensis*, *Acer tschonoskii*, *Acer japonicum* and *V. furcatum*. The mire is close to the lowermost extent of the subalpine coniferous forest zone. The *P. pumila* scrub, which dominates the summit areas in combination with *Sorbus commixta* and *Rhododendron brachycarpum*, is also found around mires at lower elevations. A mixed thicket of *A. mariesii* and shrubs is distributed on flat and poorly drained places, including the marginal area of mires (Yoshioka 1963). The mixed thicket consists of stunted *A. mariesii*, *S. commixta* and shrubs such as *A. tschonoskii*, *Quercus crispula* var. *horikawae* and *Ilex sugerokii* var. *brevipedunculata*.

Field and laboratory methods

The field survey and collection of core and surface samples for pollen analysis were conducted in August and September 2001. Permission to sample within the protection area was granted to the author by the Ministry of the Environment, Japan (No. 542; 2001).

To represent microrelief, the relative heights of the mire surface were measured along two lines (Line A and Line B) crossing the mire centre by using a surveying compass (LS-25, Ushikata Mfg. Co. Ltd., Yokohama, Japan) and staff. The vegetation of the mire, marginal scrub and thicket was surveyed at 49 plots along Lines A and B and three short subsidiary transects (Lines Ab, Ix and Qr). The sizes of the plots were 1 m × 1 m in the mire and 2 m × 2 m, 2 m × 3 m or 3 m × 3 m in the scrub and thicket. All species and their percent coverage in every plot were recorded with a modified decimal scale of 10 % increments (i.e. 10 %, 20 %, 30 %, etc.). Classes of 5 %, 1 % and + (representing an occurrence of <1 %) were employed for less abundant species. The relative coverage of each shrub and herb species was calculated afterwards on the basis of the percent coverage value of each class (class + was converted to 0.1 %). For tree elements (*Abies*, *Pinus*, *Quercus* and *Acer*) original percent coverage values were used to represent species abundance of the upper storey and to prevent sparse trees from generating aberrations in the relative coverage of the shrub and herb layers.

Surface samples containing live moss and/or undecomposed litter were collected at the centre of each quadrat for extracting modern pollen. Sediment cores penetrating through the To-a tephra that was deposited in 915 CE were collected with a Hiller-type

peat sampler (Makabe-giken, Sendai, Japan) at the same point as where the surface samples were obtained. Peat subsamples (~5 mm thick) were sliced from the cores just below the To-a tephra. Surface samples and core subsamples were prepared for pollen analysis using 10 % KOH solution to remove humic colloids and deflocculant. After sieving at 300 µm to remove coarse material, gravity separation in a solution of ZnCl₂ (specific gravity > 1.90) was carried out. The samples were then acetolysed to remove cellulose and mounted unstained in glycerine jelly. All pollen and spore grains were counted on the whole surface or in evenly spaced transects on a cover slip until the total count of tree pollen exceeded 500 at a magnification of 400×, or 1000× when necessary.

The total count including non-tree pollen and spore types ranged from 601 to 1634 grains. Percentages of tree pollen type were expressed as a proportion of the total tree pollen count to represent regional forest composition around the mire and to allow a comparison of the present and past forests. Percentages of non-tree pollen and spore types were expressed as a proportion of the sum of non-tree pollen and spore types to allow direct comparison of their percentages with those of the plant coverage present in and around the mires. Although *Castanea*-type pollen consists of *Castanea*, *Castanopsis* and/or *Lithocarpus* pollen, the northern limits of the latter two genera are more than 250 km to the south. Some pollen types were integrated (e.g. *Pterocarya/Juglans*) when it was necessary for comparison between different mires.

To discuss pollen dispersal and representation for each pollen type, similarity values using presence/absence data of modern pollen and plants in the same plot were calculated by using Davis's (1984) association index (*A*). This calculation was carried out for 48 taxa for which pollen and/or plants were present in more than 15 of 76 plots in three mires: Takada-yachi (this study), Ohse-yachi (Yonebayashi 1996) and Shimo-kenashi (Yonebayashi 2001). Davis's association index is basically the same as Jaccard's coefficient and is calculated by the formula:

$$A = c/(a + b + c) \quad [1]$$

where *c* is the number of plots where both the pollen type in the surface sample and the associated plant taxon are present, *a* is the number of plots where the pollen type is present but the associated plant taxon is absent, and *b* is the number of plots where the pollen type is absent but the associated plant taxon is present. This index can range from 1.0 to 0.0.

RESULTS

Figures 2–5 show the percent coverage of plants, modern pollen percentages and pollen percentages in 915 CE. The relative coverage of each plant species is summarised for those categories coinciding with the palynomorph classification (pollen type) to allow direct comparison between pollen and plants (Tables A1 and A2 in the Appendix). The original species composition data are provided in Table A3. Plot-based presence of modern pollen and plants, as well as the association index (A) between the pollen type and the source plants, are listed in Table A4.

Vegetation

Takada-yachi Mire is a mixed sedge-grass-*Sphagnum* bog (Tables A1–A3). It slopes slightly towards the north, with a convex profile in the east–west direction (Figure 1). The mire is enclosed with thicket and scrub, in which *A. mariesii* (A170, B-1, Ab1), *P. pumila* (A-1, B66, B68), *Q. crispula* (Qr0), *A. tschonokii* (Ab1, Ix0, Qr0), *Ilex crenata* var. *paludosa* (A-1, A168, Qr0) and/or *I. sugerokii* var. *brevipedunculata* (A170, B-1, Ab1, Ix0) are abundant. *Osmundastrum cinnamomeum* var. *fokiense*

(Osmundaceae; Ab1), *Trautvetteria caroliniensis* var. *japonica* (Ranunculaceae; Ab1), *Lysichiton camtschatcensis* (A170, Qr0) and *S. kurilensis* (Poaceae; A-1, A170, B-1, B66, B68, Ab1, Ix0) are abundant in the understorey of these communities.

Sphagnum species (including *S. tenellum*, *S. papillosum* and *S. magellanicum*) are abundant (11.0–49.4 % of total coverage) at most of the plots in the mire. *Moliniopsis japonica* (Poaceae) is often abundant both in and around the mire. Cyperaceae species (*Eriophorum vaginatum*, *Rhynchospora yasudana*, *Rhynchospora alba* and others) and *Geum pentapetalum* (Rosaceae) account for more than 10 % of coverage at many plots in the mire. *Vaccinium oxycoccos* (a creeping Ericaceae species) is common and sometimes exceeds 10 % of coverage in the mire, and shrub species of Ericaceae (*Menziesia multiflora*, *R. brachycarpum* and others) frequently appear on the fringe of the mire. *Coptis trifolia* (A140), *Sanguisorba tenuifolia* (Ix10), *Scheuchzeria palustris* (A60, A70, A80) and *Narthecium asiaticum* (A0, A1, A5, A160, A163) exceed 10 % of coverage at some plots in the mire. *Parnassia palustris* (Saxifragaceae) and *Drosera rotundifolia* are commonly found in low percentages.

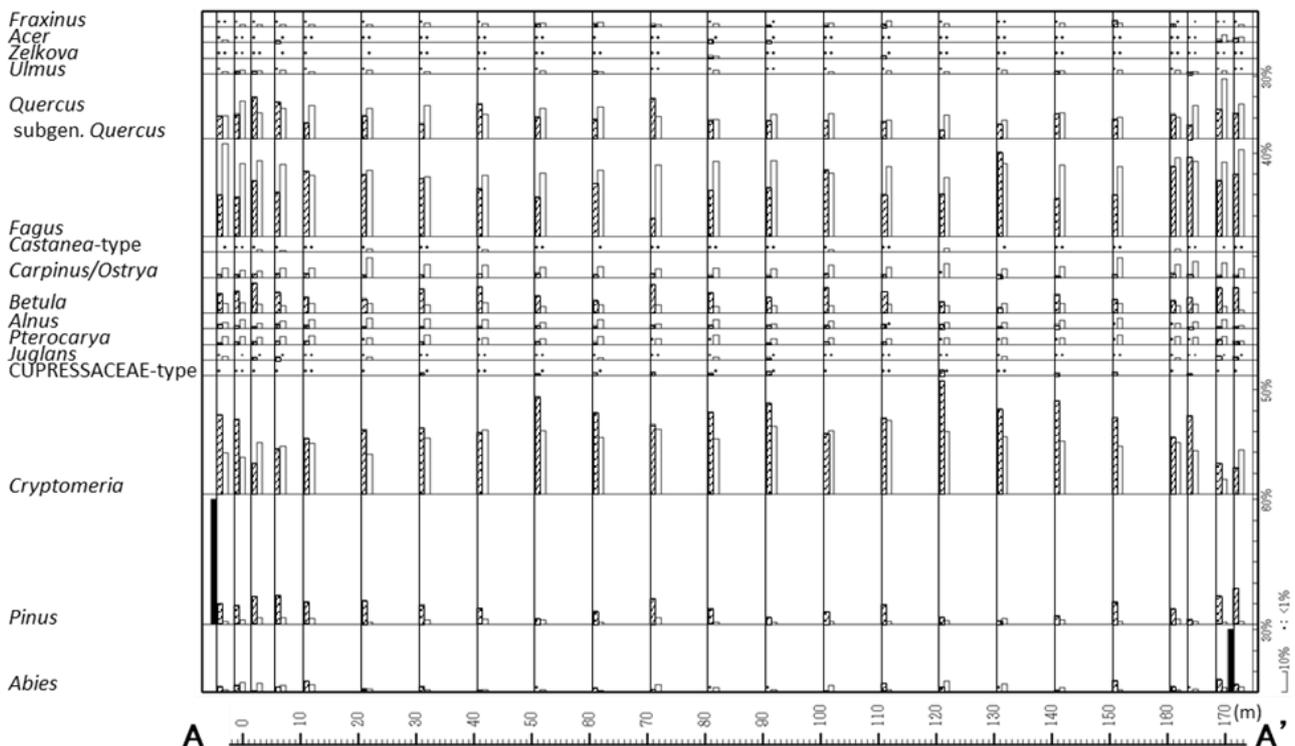


Figure 2. Diagram comparing percent coverage of plants (solid), surface pollen percentages (hatched) and pollen percentages in 915 CE (open) of selected trees on Line A. Pollen percentages are expressed as a proportion of the total tree pollen count. Plus signs in the diagram indicate abundances < 1.0 %.

Comparison between surface pollen assemblages and vegetation

Pollen of *Cryptomeria*, *Fagus* and *Quercus* was abundant, and *Pinus*, *Abies*, *Pterocarya*, *Alnus*, *Betula* and *Carpinus/Ostrya* were common among the tree pollen types (Figures 2 and 3). The proportion of tree pollen types was relatively high (55.9–78.9 %), except for Qr14 where *Sphagnum* spores occupied as much as 33.0 %. The percentages of tree pollen types were more constant among plots than those of non-tree pollen and spore types. Among the non-tree pollen and spore types, Cyperaceae was abundant and Poaceae, *Artemisia* and *Sphagnum* were common (Figures 4 and 5). Pollen of Rosaceae (excluding *Sanguisorba*) and spores of *Sphagnum* represented high percentages at some plots in the mire, whereas pollen percentages for *Lysichiton*, Poaceae and *Ilex* were high at some marginal plots.

From a plot-based comparison between surface

pollen and vegetation (Table A4 for selected taxa), pollen types of 14 trees (e.g. *Cryptomeria*, *Pterocarya/Juglans*, *Alnus*, *Carpinus/Ostrya*, *Fagus* and *Ulmus/Zelkova*), 4 shrubs (*Salix*, *Corylus*, *Ligustrum* and *Symplocos*) and 15 herbs (e.g. Chenopodiaceae/Amaranthaceae, *Artemisia* and *Typha/Sparganium*) were detected in the surface pollen assemblages but absent from the vegetation. Five trees (*Abies*, *Pinus*, *Betula*, *Quercus* and *Acer*), 5 shrubs (*Rhus/Toxicodendron*, *Ilex*, *Cornus*, *Viburnum* and Ericaceae), 14 herbs (e.g. *Drosera*, *Sanguisorba*, *Aletris/Narhecium* Poaceae, *Lysichiton* and Cyperaceae), 4 ferns and *Sphagnum* were found in the vegetation as well as pollen assemblages. Two shrubs (*Daphniphyllum* and *Orixa/Skimmia*) and 11 herbs (e.g. Diapensiaceae, Primulaceae, *Scheuchzeria* and Juncaceae) were present in the quadrats but absent from the surface pollen assemblages.

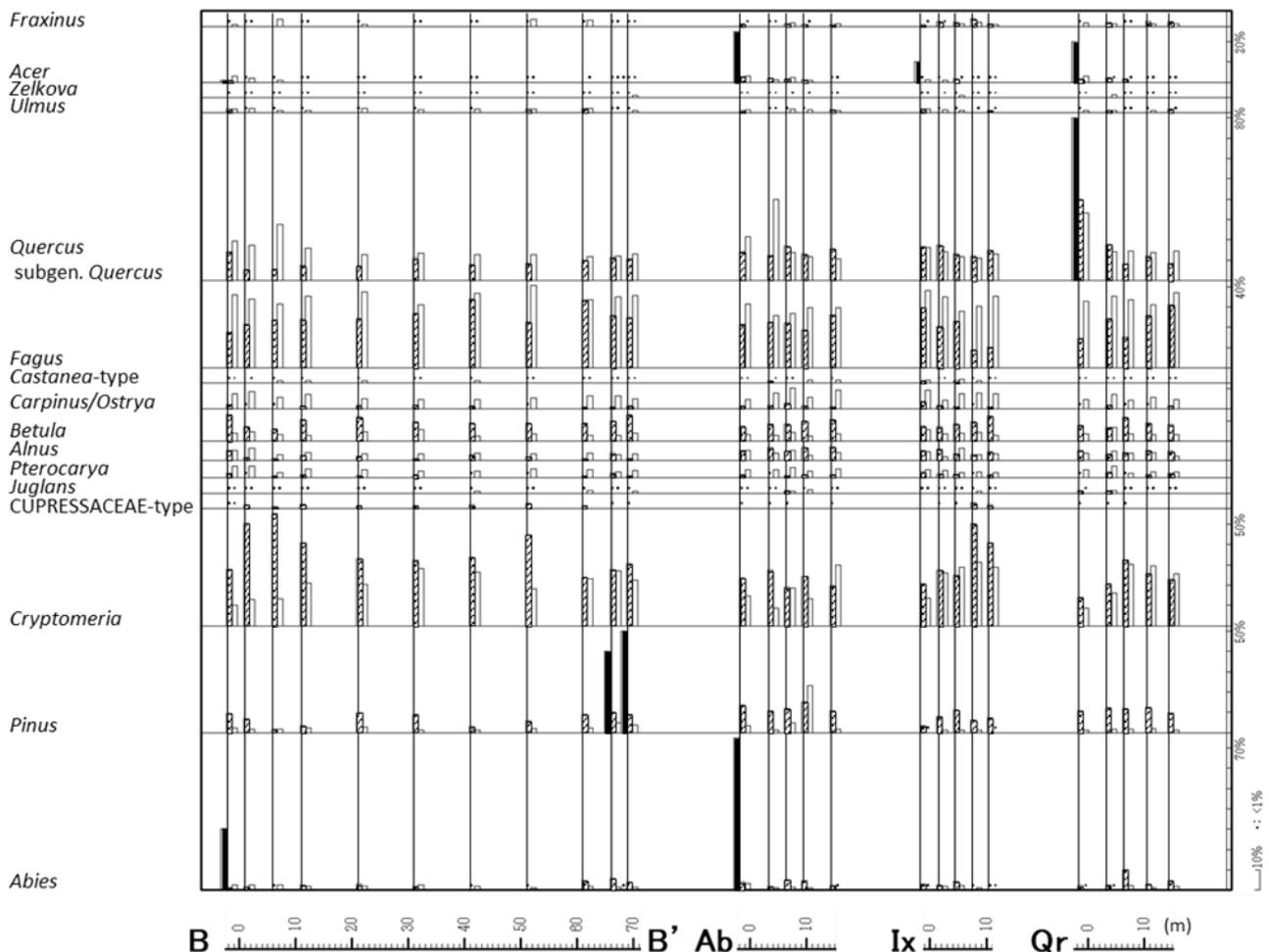


Figure 3. Diagram comparing percent coverage of plants (solid), surface pollen percentages (hatched) and pollen percentages in 915 CE (open) of selected trees on Lines B, Ab, Ix and Qr. Pollen percentages are expressed as a proportion of the total tree pollen count. Plus signs in the diagram indicate abundances < 1.0 %.

Changes in pollen assemblages from pre-tephra to modern samples

Sixty-two pollen and spore types detected just below the To-a tephra were also found in the surface samples. Ten pollen types (*Myrica*, *Viscum*, *Hamamelis*, *Zanthoxylum*, *Weigela*, *Persicaria*, Gentianaceae, Laminaceae, *Patrinia* and Campanulaceae) were detected only in the pre-tephra samples, whereas 4 pollen types (*Lysichiton*, *Bistorta*, *Fagopyrum* and Haloragaceae) occurred only in the surface samples. In the pre-tephra

samples, *Fagus*, *Cryptomeria* and *Quercus* pollen types were abundant and *Pinus*, *Pterocarya*, *Alnus*, *Betula* and *Carpinus/Ostrya* were common. Pollen percentages of deciduous broad-leaved trees such as *Fagus*, *Quercus*, *Pterocarya*, *Alnus* and *Carpinus/Ostrya* were higher than those in the surface samples, and those of subalpine conifers (*Pinus* and *Abies*) and *Betula* were lower.

The percentage values of some non-tree pollen types and *Sphagnum* spores were higher in the pre-tephra samples at some plots compared with the

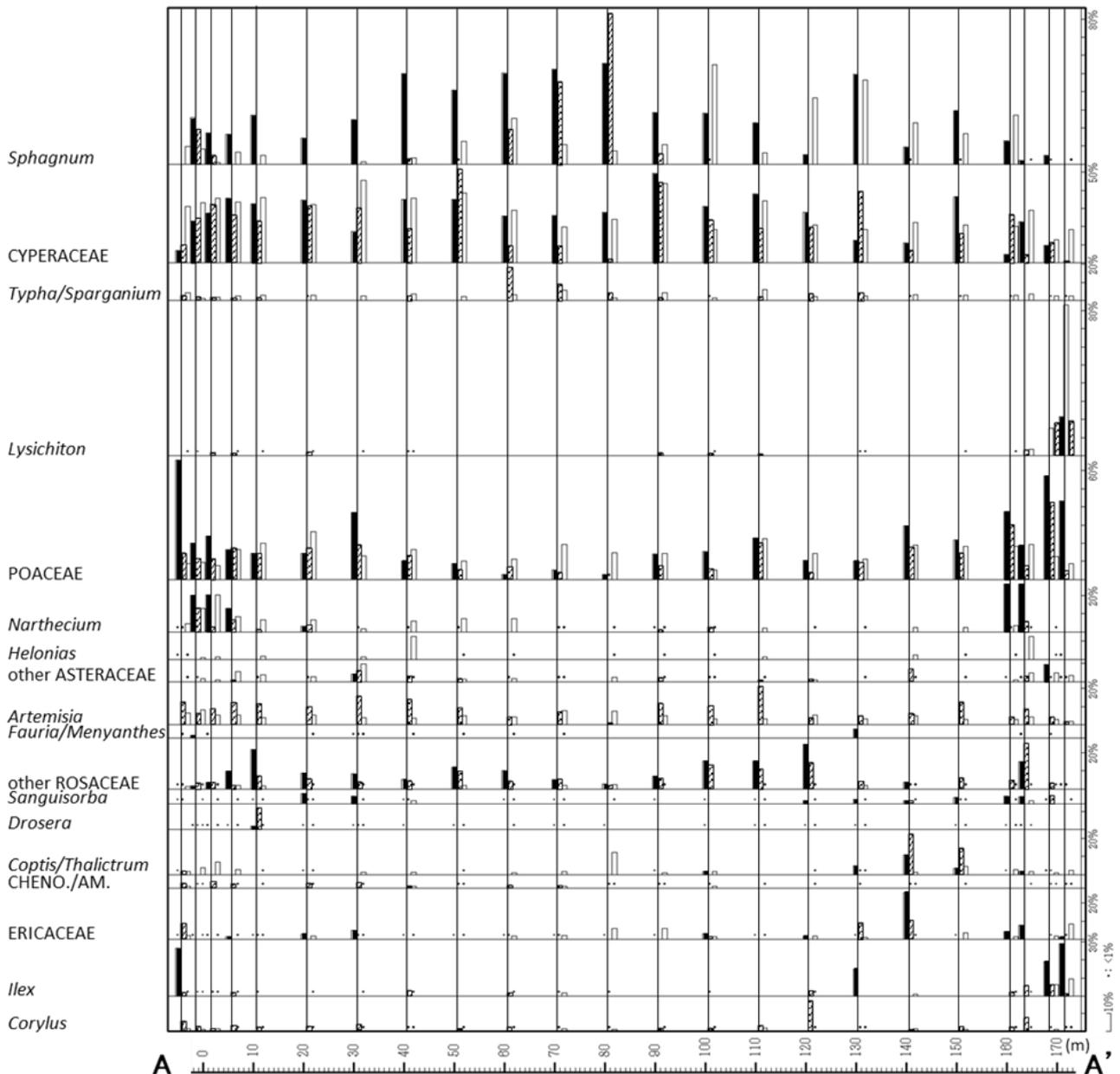


Figure 4. Diagram comparing percent coverage of plants (solid), surface pollen percentages (hatched) and pollen percentages in 915 CE (open) of selected non-trees on Line A. Pollen percentages are expressed as a proportion of the total non-tree pollen and spore count. Plus signs in the diagram indicate abundances < 1.0%. CHENO./AM. stands for CHENOPODIACEAE/AMARANTHACEAE.

modern samples. For example, Cyperaceae pollen represented higher percentages around the ends of Lines A and B (A-1, A0, A168, A170, B-1, B1, B6, B61, B66, B68), and *Sphagnum* spores were abundant at some plots in the mire (A100, A120, A130, B30, B70, Qr14). The abundance of Poaceae pollen tended to be higher in the mire and lower in the marginal plots.

DISCUSSION

In previous studies at Ohse-yachi and Shimo-kenashi Mires in the same area, I described the properties of pollen dispersal and representation from a site-based (presence/absence in a mire) comparison between the presence of plants in a vegetation survey and that of pollen at the modern surface (Yonebayashi 1996,

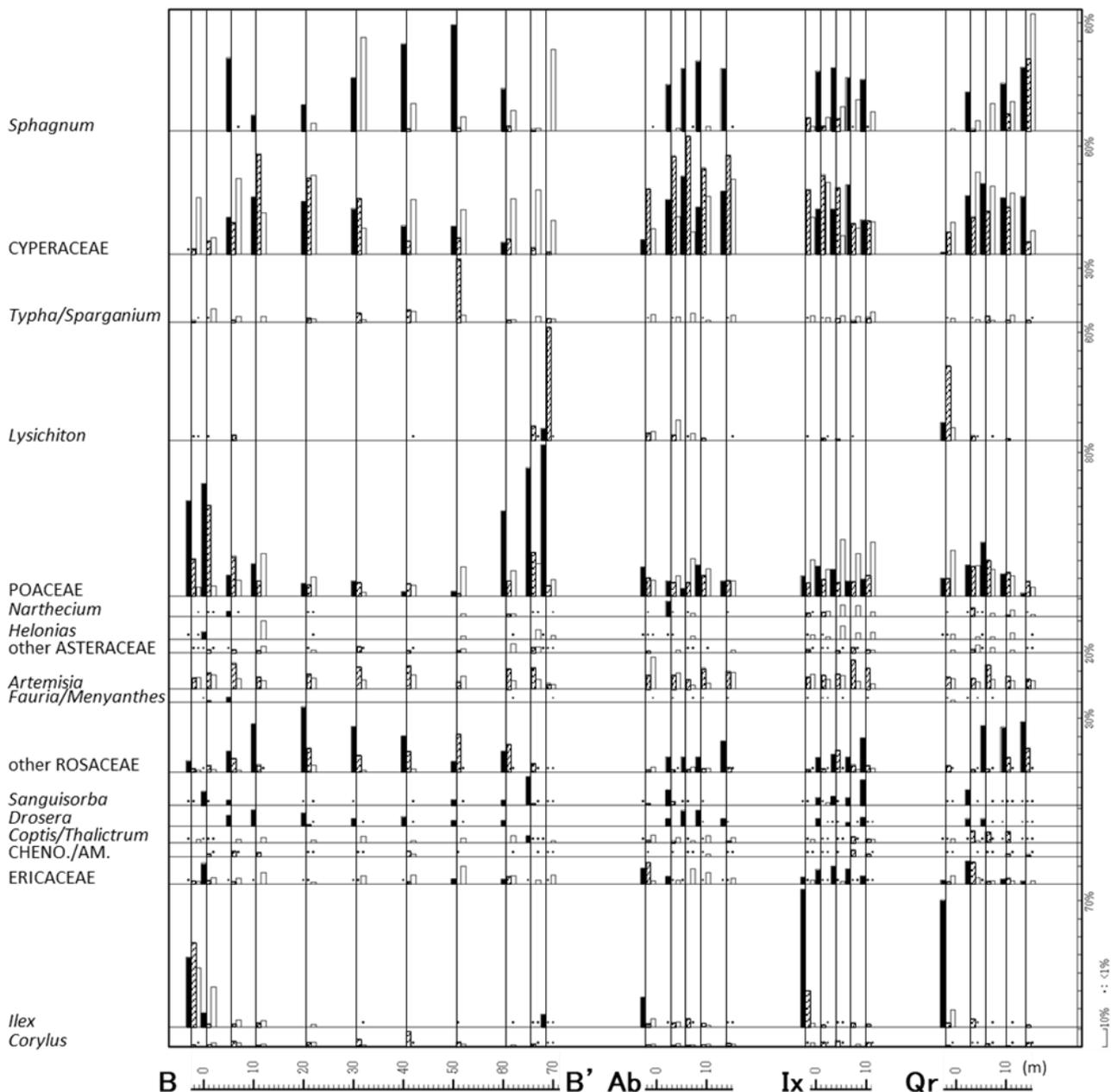


Figure 5. Diagram comparing percent coverage of plants (solid), surface pollen percentages (hatched) and pollen percentages in 915 CE (open) of selected non-trees on Lines B, Ab, Ix and Qr. Pollen percentages are expressed as a proportion of the total non-tree pollen and spore count. Plus signs in the diagram indicate abundances < 1.0 %. CHENO./AM. stands for CHENOPODIACEAE/AMARANTHACEAE.

2001). Plants were classified into the following three groups: (1) pollen present but plant absent; (2) pollen absent but plant present; and (3) both pollen and plant present. The first group, which is correlated with extra-regional, regional and extra-local components (Janssen 1981), includes most of the trees and ferns and some shrubs and herbs. The second group consists of some shrubs and herbs. The third group, which is correlated with local components (Janssen 1981), includes some trees and shrubs, various herbs and *Sphagnum*. The estimated local components and their pollen and spore dispersal efficiency considering quadrat size allowed for reconstruction of the extent and local vegetation of the mires in 915 CE.

In this study, 17 of the 48 examined taxa were categorised into different groups in different mires (Table A4). Thirteen taxa were classified as both first group (pollen present but plant absent) and third group (both pollen and plant present). The difference in this case is whether the source plants of a detected pollen type occur in the surveyed plots. This difference implies that the grouping depends on the selection and number of surveyed plots of a mire, because the chance of recording the source plants will increase with the variety and number of communities surveyed. Four herbs (*Drosera*, Saxifragaceae, *Hosta* and *Aletris/Narthecium*) were identified as both second group (pollen absent but plant present) and third group. All of these taxa are entomophilous with low pollen productivity and limited dispersal. Their pollen grains will probably not be detected by chance. Therefore, if rare pollen grains of these taxa are detected at any plot in the mire, the associated taxon will be classified as the third group, whereas if they are not detected, it will be classified as the second. The chance of detecting rare pollen types and classifying these taxa as the third group will also increase with the number of plots. In both cases, the third group (local components) will increase with the number of plots surveyed in and around a mire. Because these criteria for local component estimations are affected by the number of plots, they are unsuitable for proper estimation. To solve this problem, in this study a plot-based association index (*A*) of occurrence between surface pollen assemblage and vegetation was employed. If a taxon has a high association index, the probability that its pollen would be deposited in the same plot as the source plant is high; thus, the index reflects the probability of the coexistence of pollen and plants in a plot and is expected to be unaffected by the number of surveyed plots.

Four herbs, Ericaceae and *Sphagnum* have an association index value exceeding 0.50 (Table A4).

Among these, *Sanguisorba*, Rosaceae (excluding *Sanguisorba*), Ericaceae and *Sphagnum*, which are entomophilous or short moss with limited dispersal efficiency, were considered to be local elements in previous studies (Yonebayashi 1996, 2001). This outcome suggests that the local components estimated with the association index as well as the previous results are sound. Their pollen would rarely enter a quadrat from the outside, because their pollen was seldom detected in plots where the source plants were absent. Therefore, if their pollen is detected, the source plants are expected to be present within about 1 m (quadrat size) of the sampling point. Poaceae and Cyperaceae showed the highest and second-highest index values (1.00 and 0.92); their pollen was detected in all plots and plants occurred in all or most quadrats. Because both families are anemophilous and include many species with different ecological requirements, long-distance dispersal will contribute to pollen rain to a certain extent. Nevertheless, they should be regarded as extra-local components rather than regional components, because their pollen percentages were high in neighbouring plots where plants were abundant (Figures 4 and 5).

Ilex, *Acer* and eight herbs (Apiaceae, Saxifragaceae, *Coptis/Thalictrum*, *Aletris/Narthecium*, Asteraceae [excluding *Artemisia* and Cichorioideae], *Menyanthes/Fauria*, *Drosera* and *Lysichiton*) showed relatively high index values (0.48–0.12), although there were many plots where their pollen was present but the plant was absent. The relatively high association index implies that pollen and plants coexist with a high probability, while pollen grains also come into the quadrat from outside. Therefore, these taxa probably have a pollen dispersal efficiency exceeding the quadrat size, but the pollen seldom comes from a distance. Consequently, these taxa should be classified as local components as well as extra-local components. If their pollen grains are detected, the source plants probably exist within a few metres (larger than the quadrat size). Of these, *Drosera* was previously classified as a local component (Yonebayashi 1996).

In two cases, only pollen or the plant was observed in plots (*A* = 0). If pollen is present but the source plant is absent (first group), then all pollen grains of a taxon have come into the quadrat from the outside, and this pollen type should be correlated with non-local (extra-regional, regional and extra-local) components. This case, which is defined as “over-represented” by Davis (1984), is applicable to most trees, some shrubs (*Salix*, *Corylus*) and herbs (*Typha/Sparganium*, Moraceae/Urticaceae, Chenopodiaceae/Amaranthaceae and *Artemisia*) (Table A4). Although some trees (*Acer*, *Abies*, *Pinus*)

showed relatively high index values, this would arise from the fact that these trees sometimes grow in and around mires (but are frequently sterile in the mire). However, local deposition seems to contribute less to pollen assemblages in non-forested areas, as pollen percentages were not affected much by the existence of these trees (Figures 2 and 3). Osmundaceae, which also showed a relatively high index value, would have similar properties, because this family includes a prolific hygrophilous species (*O. cinnamomeum* var. *fokiense*). In the second case, pollen is absent but the plant is present (second group), which was defined as “under-representation” (Davis 1984). This was applicable to some herbs (e.g. Juncaceae, Diapensiaceae) and shrubs (e.g. *Orixa/Skimmia* and *Viburnum*; not shown in Table A4). Their pollen grains may never be detected because of the species’ low pollen productivity, limited dispersal efficiency, poor preservation and/or identification difficulty.

Vegetation in 915 CE compared with the present

The level just below the To-a tephra is considered to be a continuous surface layer at 915 CE (Yonebayashi 1996). If the rate of deposition of the peat between To-a and To-Cu (5986–5899 cal. year BP; McLean *et al.* 2018) at the Takada-yachi Mire was constant, it is estimated to be about 0.15–0.17 mm year⁻¹ based on the dates of the tephra falls and the peat depths between the two (75–83 cm; Morita 1982). Therefore, the pollen assemblages collected from the 5-mm-thick subsample just below the To-a tephra account for an average of 30–33 years of pollen deposition. This time span is similar to that of Ohse-yachi Mire (25–50 years) and smaller than that of Shimo-kenashi Mire (25–125 years).

High percentages of *Cryptomeria* pollen type in the surface samples probably resulted from an expansion of *C. japonica* plantations at lower altitudes after World War II. The percentages of *Fagus* and *Quercus* pollen types were generally higher in pre-tephra samples (17.4–32.7 % and 5.5–30.1 %, respectively) than in surface samples (8.7–40.5 % and 4.4–20.0 %), indicating that the regional vegetation around the mire was montane broad-leaved forest dominated by *F. crenata* and *Q. crispula* in 915 CE. In contrast, the percentages of subalpine components such as *Abies*, *Pinus* and *Betula* were generally lower in the pre-tephra samples than in the surface samples. The regional *A. mariesii* subalpine forest in the Hakkoda Mountains markedly expanded after the To-a fall (Morita 1987).

Among the four local elements mentioned earlier, *Sphagnum* spores were higher in terms of both frequency (number of plots where a pollen type

occurred) and percentages in the mire just below the To-a tephra. This result suggests that *Sphagnum* species (e.g. *S. tenellum*, *S. papillosum* and *S. magellanicum*) were more common and abundant in 915 CE. Compared with present values, Rosaceae (excluding *Sanguisorba*) pollen type had a lower percentage in the pre-tephra samples, but the frequency has hardly changed. This finding suggests that the mire has become drier and that *G. pentapetalum*, which is abundant in many plots in the present mire, has increased in abundance. Because Ericaceae and *Sanguisorba* pollen types were more frequent in the pre-tephra samples, *V. oxycoccos* and *S. tenuifolia* would have been more common in the mire in 915 CE.

Ilex, *Acer* and *Lysichiton* were estimated to have attributes of both local and extra-local elements and may serve as mire-margin indicators. Among the source plants, *I. crenata* var. *paludosa* and *I. sugerokii* var. *brevipedunculata* form the marginal scrub, *Acer* spp. are often abundant in thickets with stunted trees and *L. camtschatcensis* is common in soggy depressions at the fringe of the mire. Therefore, the occurrence of these pollen types can indicate the position of the mire margin with an accuracy of a few metres. *Ilex* pollen type was rare around the margin (A-1, A163, Ix0, Qr3) in pre-tephra samples and increased at the modern surface. Given that pollen dispersal efficiency was within a few metres, *Ilex* scrub has probably advanced up to about 5 m and the mire vegetation retreated around the plots. However, retreat of *Ilex* scrub, indicated by upwards pollen decline, was inferred around the mire’s northern margin (B1, B6, B11, Ab1). An upwards increase in *Lysichiton* pollen percentages around the margin (A170, B66, B68, Qr0) also indicates the retreat of mire plants in place of the advance of *L. camtschatcensis* at the fringe of the mire. *Acer* does not show a significant tendency to change in the marginal position, because its pollen type occurred in most plots in low percentages in both the surface and pre-tephra samples. Changes in the pollen representation of *Ilex* and *Lysichiton* indicate retreat of the mire around both ends of Line A, and around the southern ends of Line B and the short lines Ix and Qr; whereas mire advance is suggested around the depressed northern ends of Lines B and Ab. The slight retreats of the mire were probably caused by drying, as suggested by the increase in Rosaceae. However, the advance around the depressed northern margin probably indicates retrogressive succession controlled by local hydrology, such as an accumulation of volcanic acid water and anaerobic conditions resulting from the lack of drainage. In the early 1940s, some ecologists noted the retrogressive

succession from a forest community to wet mire in this area (Yoshii & Yoshioka 1940, Iwata 1941). Iwata (1941) observed that the growth of *A. mariesii* had deteriorated and some individuals were dying at two communities on a mire located about 300 m SSW of the mire of this study; moreover, wet mire components such as *R. yasudana*, *V. oxycoccus* and *Sphagnum* had invaded the understoreys of the woods. The pollen evidence from the northern end of the mire of the present study supports these observations.

My analyses indicate that the Takada-yachi Mire was a wetter *Sphagnum* mire in 915 CE and has changed to the present-day drier one. The extent of the mire has retreated about 5 m at maximum, although the margin around the depressed northern end has slightly expanded. Nevertheless, the mire maintains peatland with a similar size today as that during the last millennium. Although macrofossil analysis is beyond the scope of this study, it will help to better reconstruct the local vegetation.

Implications for conservation

Although the Takada-yachi, Shimo-kenashi and Ohse-yachi Mires are montane oligotrophic mires of similar physiognomy in the same mountains, their vegetation histories during the last millennium differ. The Takada-yachi and Ohse-yachi Mires (Yonebayashi 1996) were wetter in 915 CE and have become drier, whereas the Shimo-kenashi Mire was drier and has expanded to the present margin (Yonebayashi 2001). The contrasting vegetational histories among these mires confirm the idea that local mire vegetation is primarily controlled by local factors such as the local hydrology and microrelief of the mire (Yonebayashi 2001). Faber *et al.* (2016) reported different peatland vegetation histories on the order of centuries, along with implications for management, in two former turbaries in the Netherlands. The conservation of mires with unique vegetation histories will therefore require different procedures. The Takada-yachi and Ohse-yachi Mires are fairly well preserved, because hikers seldom visit there. Although the mires have become drier from a millennium-scale perspective, further management measures are not needed to maintain the present vegetation. But human-induced disturbance threatens the natural ecosystem of the Shimo-kenashi Mire that is on a main trekking route. Although this mire has become wetter and expanded from a long-term perspective, recent surface water flow along wood trails seems to cause erosion and drying out. Hence, making weirs in the eroded ditch would be efficient to prevent the mire from drying out.

This study provides empirical evidence of the

millennium-scale changes in a mire ecosystem, highlighting the question of ‘What is natural?’ (Willes & Birks 2006). This evidence can be used to help decide what the mire should be in the future and to evaluate the results of human activities in terms of conservation.

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Author for correspondence:

Professor Chuh Yonebayashi, Faculty of Geo-Environmental Science, Rissho University, Magechi 1700, Kumagaya, Saitama 360-0194, Japan. Tel: +81-48-5391643; E-mail: cyone@ris.ac.jp

Appendix

Table A1. Species composition of the plots on Line A in Takada-yachi Mire. The relative cover of each taxon is summarised for those categories coinciding with the pollen type. The extent of species dominance is shown as original percent coverage for trees and relative coverage for non-trees.

Plot No.	A-1	A0	A1	A5	A10	A20	A30	A40	A50	A60	A70	A80	A90	A100	A110	A120	A130	A140	A150	A160	A163	A168	A170	
Trees																								
<i>Abies</i>																								30.0
<i>Pinus</i>	60.0																							
<i>Quercus</i>																								
<i>Acer</i>																								1.0
Non-trees																								
<i>Orixa/Skimmia</i>																								0.7
<i>Rhus/Toxicodendron</i>																								
<i>Ilex</i>	26.3																14.9						19.0	28.8
<i>Cornus</i>																								
ERICACEAE	0.3	0.1	0.3	1.6	0.4	2.9	4.9	+	0.6	0.6	0.1	0.1	0.1	3.1	0.1	1.7	0.5	25.7	0.7	4.4	7.9			1.0
<i>Coptis/Thalictrum</i>	0.1					+							0.1	1.6			5.0	11.0	3.6	0.4	1.9	0.1		
other RANUNCULACEAE																								
<i>Drosera</i>		+	0.3	0.3	1.8	0.3	0.1	+	0.1		0.1	0.1		0.3	0.1	0.3	+		0.7	+	+			
SAXIFRAGACEAE			0.3	0.3	0.4	1.4	0.1	+	0.1	0.5	0.1		0.1	1.6	0.1	0.3	+	0.4	0.1	0.4	0.4	0.1		
<i>Sanguisorba</i>	0.1				+	5.8	4.1	+		0.1	0.5		0.1	0.3	0.1	1.7	2.5	1.8	3.6	4.4	3.8	0.1		
other ROSACEAE	0.1	1.4	3.4	9.8	21.6	8.7	8.2	5.0	11.7	10.1	5.2	2.8	7.1	15.5	15.3	24.4		3.7				15.1		0.7
APIACEAE																								
GENTIANACEAE																								
<i>Fauria/Menyanthes</i>		1.4	+				0.1										5.0					+		
RUBIACEAE																								
other ASTERACEAE							4.1													+	0.1	9.6	0.1	
<i>Scheuchzeria</i>									0.1	10.1	10.4	11.1												
<i>Heloniopsis</i>	0.1																							0.1
<i>Hosta</i>																								
<i>Narthecium</i>	0.1	20.0	20.5	13.0		2.9							0.7									26.2	26.4	
other LILIACEAE		8.6	6.8			1.4								+								0.4		0.1
JUNCACEAE				3.3	1.8	1.4			2.9					3.1	0.1	7.0								
POACEAE	65.8	20.0	23.9	16.3	14.4	14.4	36.7	10.0	8.7	2.5	5.2	2.8	14.1	15.5	23.0	10.4	10.0	29.4	21.7	37.1	18.9	56.9	43.1	
<i>Lysichiton</i>																								21.5
CYPERACEAE	6.7	22.8	27.3	35.8	32.4	34.7	17.3	34.9	35.1	25.7	26.1	27.7	49.4	31.0	38.3	27.9	12.4	11.0	36.2	4.8	22.7	9.5		
<i>Lycopodium</i>																								0.1
OSMUNDACEAE																								3.6
monolete fern spore																								0.1
<i>Sphagnum</i>		25.7	17.1	16.3	27.0	14.4	24.5	49.9	40.8	50.5	52.2	55.5	28.3	27.9	23.0	5.2	49.6	9.6	29.7	13.1	1.9	4.7		
unidentified/undetectable	0.3	+	+	3.3	0.4	11.6			0.1				0.2	+	0.2	20.9	0.1	7.4	0.1	9.2	0.5			0.1

Table A2. Species composition of the plots on Lines B, Ab, Ix and Qr in Takada-yachi Mire. The relative cover of each taxon is summarised for those categories coinciding with the pollen type. The extent of species dominance is shown as original percent coverage for trees and relative coverage for non-trees.

Plot No.	B-1	B1	B6	B11	B21	B31	B41	B51	B61	B66	B68	Ab1	Ab3	Ab6	Ab9	Ab14	Ix0	Ix1	Ix4	Ix7	Ix10	Qr0	Qr3	Qr10	Qr14	
Trees																										
<i>Abies</i>	30.0										0.1	75.0														
<i>Pinus</i>										40.0	50.0															
<i>Quercus</i>																						79.9				
<i>Acer</i>	1.0										0.1	25.0					10.1					20.1				
Non-trees																										
<i>Orixa/Skimmia</i>	0.1										1.4	0.2					0.1					0.1				
<i>Rhus/Toxicodendron</i>	0.1																									
<i>Ilex</i>	38.8	7.8									7.0	16.4	+				76.6					70.4				
<i>Cornus</i>												8.1														
ERICACEAE	0.8	11.7	0.1	0.9	0.1	+	0.1	3.2	3.0	0.1		9.1	4.3	+		+	4.1	8.3	10.0	8.5	4.8	2.2	13.0	3.1	1.8	
<i>Coptis/Thalictrum</i>	0.1	0.1									4.0	0.1	0.2									0.1	+	0.3	0.0	
other RANUNCULACEAE												16.2										0.1				
<i>Drosera</i>			5.8	9.0	7.3	4.2	5.1	3.1	3.0			4.3	8.7	8.7	4.3		4.2	+	2.1	4.8		4.3	+	0.4		
SAXIFRAGACEAE		0.1	0.6		3.6	2.1	2.5	0.6	0.6	0.1				+									+	0.3	0.4	
<i>Sanguisorba</i>	0.1	7.8	2.9		0.1	+		3.1	3.0	15.8		0.2	8.7	+			0.1	4.2	5.0	4.3	14.3		8.6	0.3	+	
other ROSACEAE	6.5	0.8	11.7	27.0	36.3	25.5	20.4	6.2	11.9				8.7	8.7	8.7	17.4		8.3	10.0	8.5	19.0			25.1	28.1	
APIACEAE																						0.1				
GENTIANACEAE												8.1						3.8								
<i>Fauria/Menyanthes</i>		0.8	2.9																				+			
RUBIACEAE																						0.1				
other ASTERACEAE		0.8	0.1								0.1															
<i>Scheuchzeria</i>					0.1	4.2	5.1	6.2																		
<i>Heloniopsis</i>	0.1	3.9									0.1	0.2	+									0.1				
<i>Hosta</i>										7.9	0.1	0.2	+				3.8					0.1	2.2			
<i>Narthecium</i>			2.9										8.7										0.4			
other LILIACEAE				4.5	0.7					0.1	0.1	0.3										0.3				
JUNCACEAE															+	+							+		+	
POACEAE	53.0	62.4	11.7	18.0	7.3	8.5	2.6	3.1	47.6	71.2	83.9	16.2	8.7	4.3	17.4	8.7	11.6	16.7	15.0	8.5	9.6	10.0	17.3	12.6	1.8	
<i>Lysichiton</i>											7.0											10.0				
CYPERACEAE	0.1		20.4	31.6	29.2	25.5	15.8	15.5	6.5			8.1	30.4	43.4	26.1	34.8		25.0	25.0	38.3	19.0	1.0	32.4	31.5	32.0	
<i>Lycopodium</i>																						0.1				
OSMUNDACEAE												16.4										5.0				
monolete fern spore																										
<i>Sphagnum</i>			40.9	9.0	14.5	29.8	48.4	59.0	23.8				26.0	34.7	39.1	34.8		33.3	35.0	29.8	28.6		21.6	26.7	35.5	
unidentified/undetectable	0.3	3.9	0.1	0.1	0.7	+	0.1		0.7	0.9		0.2	+									0.2				

Table A4. The number of plots where surface pollen (p) and plants (v) occurred, and the similarity (A: association index) between pollen assemblage and vegetation. Only pollen types for which the pollen and/or plant occurred in more than 15 plots in the three mires are represented.

Pollen and spore type		Ohse-yachi Mire (n=12)					Shimo-kenashi Mire (n=15)					Takada-yachi Mire (n=49)					Total (n=76)				A
		p, v	p, -	-, v	-, -	gr.	p, v	p, -	-, v	-, -	gr.	p, v	p, -	-, v	-, -	gr.	p, v	p, -	-, v	-, -	
POACEAE	Herb	12	0	0	0	III	15	0	0	0	III	49	0	0	0	III	76	0	0	0	1.00
CYPERACEAE	Herb	12	0	0	0	III	14	1	0	0	III	44	5	0	0	III	70	6	0	0	0.92
other ROSACEAE	Herb	6	0	4	2	III	10	3	1	1	III	39	10	0	0	III	55	13	5	3	0.75
<i>Sphagnum</i>	Moss	11	0	1	0	III	11	2	1	1	III	22	2	17	8	III	44	4	19	9	0.66
ERICACEAE	Shrub	10	0	1	1	III	7	1	4	3	III	28	3	18	0	III	45	4	23	4	0.63
<i>Sanguisorba</i>	Herb	9	1	2	0	III	0	0	0	15	-	17	3	19	10	III	26	4	21	25	0.51
APIACEAE	Herb	10	2	0	0	III	0	1	0	14	I	1	9	0	39	III	11	12	0	53	0.48
SAXIFRAGACEAE	Herb	0	0	9	3	II	3	4	6	2	III	25	15	7	2	III	28	19	22	7	0.41
<i>Coptis/Thalictrum</i>	Herb	3	6	1	2	III	2	7	1	5	III	13	9	7	20	III	18	22	9	27	0.37
<i>Aletris/Nartheicum</i>	Herb	0	0	1	11	II	0	0	9	6	II	10	18	2	19	III	13	16	18	29	0.28
<i>Ilex</i>	Shrub	1	9	0	2	III	2	8	1	4	III	10	25	1	13	III	13	42	2	19	0.23
other ASTERACEAE	Herb	5	7	0	0	III	1	7	1	6	III	7	29	2	11	III	13	43	3	17	0.22
<i>Menyanthes/Fauria</i>	Herb	4	5	0	3	III	1	2	3	9	III	2	9	6	32	III	7	16	9	44	0.22
<i>Drosera</i>	Herb	2	0	9	1	III	0	0	9	6	II	9	0	27	13	III	11	0	45	20	0.20
<i>Lysichiton</i>	Herb	0	3	0	9	I	3	8	0	7	III	3	25	0	21	III	6	36	0	37	0.14
<i>Acer</i>	Tree	0	12	0	0	I	3	11	0	1	III	6	42	0	1	III	9	65	0	2	0.12
<i>Abies</i>	Tree	0	12	0	0	I	2	13	0	0	III	4	45	0	0	III	6	70	0	0	0.08
OSMUNDACEAE	Fern	0	8	0	4	I	0	7	0	8	I	2	12	1	34	III	2	27	1	46	0.07
<i>Pinus</i>	Tree	0	12	0	0	I	2	13	0	0	III	3	46	0	0	III	5	71	0	0	0.07
other LILIACEAE	Herb	5	4	2	1	III	1	1	4	9	III	0	0	12	37	II	1	8	7	60	0.06
<i>Hosta</i>	Herb	0	0	7	5	II	0	0	5	10	II	1	0	6	42	III	1	0	18	57	0.05
<i>Rhus/Toxicodendron</i>	Shrub	0	7	0	5	I	1	3	0	11	III	0	8	1	40	III	1	18	1	56	0.05
<i>Quercus</i>	Tree	0	12	0	0	I	1	14	0	0	III	1	48	0	0	III	2	74	0	0	0.03

C. Yonebayashi MILLENNIUM-SCALE CHANGES IN MIRE VEGETATION RECONSTRUCTED

Pollen and spore type		Ohse-yachi Mire (n=12)					Shimo-kenashi Mire (n=15)					Takada-yachi Mire (n=49)					Total (n=76)				A
		p, v	p, -	-, v	-, -	gr.	p, v	p, -	-, v	-, -	gr.	p, v	p, -	-, v	-, -	gr.	p, v	p, -	-, v	-, -	
<i>Lycopodium</i>	Fern	0	8	0	4	I	1	7	2	5	III	0	19	2	28	III	1	34	4	37	0.03
ARALIACEAE	Herb	0	7	0	5	I	1	9	0	5	III	0	23	0	26	I	1	39	0	36	0.03
other trilete	Fern	0	12	0	0	I	0	15	0	0	I	1	28	2	18	III	1	55	2	18	0.02
monolete	Fern	0	12	0	0	I	0	15	0	0	I	1	40	0	8	III	1	67	0	8	0.01
<i>Betula</i>	Tree	0	12	0	0	I	1	14	0	0	III	0	49	0	0	I	1	75	0	0	0.01
<i>Cryptomeria</i>	Tree	0	12	0	0	I	0	15	0	0	I	0	49	0	0	I	0	76	0	0	0.00
CUPRESSACEAE-type	Tree	0	3	0	9	I	0	0	0	15	-	0	45	0	4	I	0	48	0	28	0.00
<i>Pterocarya/Juglans</i>	Tree	0	12	0	0	I	0	15	0	0	I	0	49	0	0	I	0	76	0	0	0.00
<i>Alnus</i>	Tree	0	12	0	0	I	0	15	0	0	I	0	49	0	0	I	0	76	0	0	0.00
<i>Carpinus/Ostrya</i>	Tree	0	12	0	0	I	0	15	0	0	I	0	49	0	0	I	0	76	0	0	0.00
<i>Castanea</i> -type	Tree	0	10	0	2	I	0	6	0	9	I	0	41	0	8	I	0	57	0	19	0.00
<i>Fagus</i>	Tree	0	12	0	0	I	0	15	0	0	I	0	49	0	0	I	0	76	0	0	0.00
<i>Cyclobalanopsis</i>	Tree	0	7	0	5	I	0	2	0	13	I	0	7	0	42	I	0	16	0	60	0.00
<i>Celtis/Aphananthe</i>	Tree	0	1	0	11	I	0	6	0	9	I	0	11	0	38	I	0	18	0	58	0.00
<i>Ulmus/Zelkova</i>	Tree	0	12	0	0	I	0	12	0	3	I	0	49	0	0	I	0	73	0	3	0.00
<i>Aesculus</i>	Tree	0	11	0	1	I	0	7	0	8	I	0	35	0	14	I	0	53	0	23	0.00
<i>Fraxinus</i>	Tree	0	12	0	0	I	0	11	0	4	I	0	47	0	2	I	0	70	0	6	0.00
<i>Salix</i>	Shrub	0	9	0	3	I	0	5	0	10	I	0	38	0	11	I	0	52	0	24	0.00
<i>Corylus</i>	Shrub	0	12	0	0	I	0	12	0	3	I	0	47	0	2	I	0	71	0	5	0.00
JUNACEAE	Herb	0	0	6	6	II	0	0	0	15	-	0	0	12	37	II	0	0	18	58	0.00
<i>Typha/Sparganium</i>	Herb	0	7	0	5	I	0	0	0	15	-	0	43	0	6	I	0	50	0	26	0.00
MORACEAE/URTICACEAE	Herb	0	0	0	12	-	0	0	0	15	-	0	33	0	16	I	0	33	0	43	0.00
CHENOPODIACEAE/AMARANTHACEAE	Herb	0	11	0	1	I	0	6	0	9	I	0	39	0	10	I	0	56	0	20	0.00
DIAPENSIACEAE	Herb	0	0	1	11	II	0	0	5	10	II	0	0	10	39	II	0	0	16	60	0.00
<i>Artemisia</i>	Herb	0	12	0	0	I	0	15	0	0	I	0	49	0	0	I	0	76	0	0	0.00

