Effects of Drainage on Open-water mire pools: Open water shrinkage and Vegetation change of Pool plant communities

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Abstract Open-water mire pools play an important role in sustaining biodiversity. However, many mire pools have disappeared by artificial drainage all over the world. This study aimed at exploring how mire pools are changed by artificial drainage in terms of open water area and vegetation in Shizukari Mire, Hokkaido. We analyzed the changes of drainage ditches and open water of mire pools using multi-temporal aerial photographs. In order to elucidate how pool plant communities change by drainage, we analyzed the vegetation on the persisting pools and drained area of former pools. Our results indicated that most pools were lost soon after digging of ditches, and the remaining pools have shrunk by more diffuse, continued drainage effect. Due to open water loss, pool plant communities were considered to change towards the plant communities of drier conditions, comprising woody plants and non-wetland plant species. If the drainage continues, the remaining mire pools will ultimately disappear and the species composition of the mire could become more homogenous, being dominated by few species with high coverage.

Keywords Continued drainage · Drainage ditch · Mire pools · Open water · Vegetation change

Introduction

Mires have been considered as rather stable ecosystems that show slow changes in vegetation over time than any other terrestrial ecosystems (Weber 1902; Backéus 1972; Svensson 1988; Zobel 1988; Klinger 1996; Malmer et al. 1997; Rydin and Barber 2001; Gunnarsson et al. 2002). However, several studies have documented relatively large responses of mire vegetation to human-induced changes in recent decades (e.g. Lee et al. 1990; Chapman and Rose 1991; Hogg et al. 1995; Gunnarsson et al. 2000; Gunnarsson et al. 2002; Gunnasson and Flodin 2007; Mälson et al. 2008; van der Linden et al. 2008). Drainage, that is the main factor of wetland loss, is frequently linked to lowering of water table, changes in stream discharge, reduction in area of wetlands, and altered composition of vegetation and wildlife species (Skaggs et al. 1994; Spaling and Smit 1995). Furthermore, the repetitive nature and areal expansion of drainage may result in accumulation of environmental changes over time and across space (Spaling and Smit 1995). In the non-tropical world, 50% of the original peatland loss is due to drainage for agriculture, and 30% is due to drainage for forestry (Joosten and Clarke 2002; Hedberg et al. 2012).

There are many previous studies about effects of drainage on vegetation and plant composition in wetlands, especially mires and peatlands (e.g. Vasander 1982; Heikkilä and Lindholm 1995a, b; Laine et al. 1995; Minkkinen et al. 1999; Joosten and Clarke 2002; Pellerin and Lavoie 2003; Pakalnis et al. 2009; Talbot et al. 2010; Laine et al. 2011). According to these studies, drainage induces secondary succession in mire vegetation and usually enhances shrub and tree encroachment and mire vegetation are replaced by common forest species. It also hampers *Sphagnum* growth and facilitates the establishment of generalist species. Of the original peatland vegetation, hummock species benefit from the drainage, while species demanding prolonged inundated conditions soon disappear after the drainage.

However, there is no study that elucidates how drainage ditch affects open-water mire pools and their vegetation. Open-water pools are a common feature of many peatlands (Walker 1961; Glaser 1998), and mire pools occur in raised mire systems in both upland and lowland locations (Heathwaite and Göttlich 1993). Mire pools play an important role in sustaining biodiversity, and are regarded as hotspots for biodiversity in peatlands (Lindsay et al. 1985; Guinan et al. 1998; Poulin et al. 2002; Fontaine et al. 2007; Kilroy et al. 2007). Moreover, peatlands including pools provide numerous ecosystem services such as carbon and nutrient sinks and flood regulators (Devito and Dillon 1993; Roulet et al. 2007). In spite of their functions, many mire pools have disappeared with peatlands due to drainage. Pools are particularly vulnerable to peatland exploitation or conversion, and will generally not return unless measures are planned specifically for them (Mazerolle et al. 2006). Recently, as recognizing the significance of the mire pools for biodiversity, there are some studies on restoration of mire pools (e.g. Mazerolle et al. 2006; Fontaine et al. 2007; Poulin et al. 2011; Beadle et al. 2015). However, natural and newly created pools had different floristic composition, although created pools potentially provide valuable new habitat for aquatic species. The studies on restoration stressed that remaining mire pools must be preserved from human disturbances, and more knowledge about the ecology of pools through the studies for restoration is needed.

Our study aimed at exploring how mire pools are changed by artificial drainage in terms of open water area and plant communities. The first objective of this study was to ascertain surface water change of mire pools caused by drainage ditches through analysis of multi-temporal aerial photographs. The second objective was to elucidate effects of drainage on plant communities through vegetation survey on persisting pools and drained area of former pools. We show how pool plant communities have changed due to drainage, and discuss how they may change henceforward if draining is continued.

Methods

Study area

Shizukari Mire (42°34′N, 140°26′E, approximately 4–5 m a.s.l.) is located along the south-western Pacific coast of Hokkaido Island in Japan (Fig. 1). The southern limit of lowland bogs of Hokkaido is situated in the southwest part of the island, somewhat further north than the line suggested by the temperature conditions (Wolejko and Ito 1986), and this area is the southernmost site with lowland bog vegetation in Hokkaido. The mean annual temperature (1978–2015) at the nearest meteorological station (6.3 km distant from the mire, 10 m a.s.l.) is 7.4°C and mean annual precipitation is 1277 mm (Japan Meteorological Agency 2016). Summers have foggy days with cover of sea fog from the Pacific Ocean (Fujita and Tachibana 1998).

Shizukari Mire was designated as a national natural monument in 1922 because it was a typical well-developed *Sphagnum* bog, and had high richness of bog plant species (Yoshii and Kudo 1926). There were a lot of bog ponds and pools in Shizukari Mire, and many floating islands were found on a largest pond between sand dunes (Tatewaki

1924; Yoshii and Kudo 1926). Various plant community types were found at the *Sphagnum* lawn and hollow, poor or rich fen, alder and ash swamp forest (Tatewaki 1924; Yoshii and Kudo 1926). The area of this mire was approximately 263 ha (excluding coastal dune part), calculated from 1/50000 topographical map of the Geospatial Information Authority of Japan issued in 1917 (Fujita and Tachibana 1998) (Fig. 2a). Although this mire had a beautiful landscape and high scientific value, it lost its status as the national natural monument in 1951 for the national policy after World War II. Simultaneously, the mire was rapidly developed and had been converted into agricultural land. Consequently, the area of the current remaining mire part is about 34 ha (Fujita and Tachibana 1998) (Fig. 2a). Most of the ponds, pools, and floating islands had disappeared, and most area of peatlands had been lost, because all the five rivers flowing into the former mire were directly connected to the drainage ditches. The current remaining mire is small part of the center portion of the former bog and includes some pool vegetation, and the surroundings are roads, drainage ditches, woodlots and agricultural lands (Figs. 2a, c). This mire is a private property owned by many owners, and no conservation activities or related policies have been conducted. Nevertheless, this mire has been recently listed as one of the "Important wetlands in Japan", because it is valuable habitat for various species established in the coastal plain (Ministry of the Environment of Japan 2016).

Analysis of multi-temporal aerial photographs

We analyzed multi-temporal aerial photographs from 1947, 1965, 1976 and 2007 (black and white pictures of 1947, 1965 and color pictures of 1976, 2007) by using the software ArcMap 10.1 in ArcGIS (ESRI 2013). We decided the analysis range (122.6 ha) by comparing the changes of open water between 1947 and 2007 (Fig. 2b), and then created polygons of open water area and lines of drainage ditches from the four aerial photographs in the range respectively. For analyzing the changes of the drainage ditches and open water area, we calculated the total length of the lines and the total area of the polygons respectively using ArcGIS.

In order to analyze the changes in a higher spatial resolution, we divided the range into 5 m × 5 m mesh; the polygons of open water area were also divided into 5 m × 5 m mesh by using the 'Intersect' tool from the analysis toolbox as overlap with the range's mesh. We defined open water grid cell as a grid cell that contains even a little area of open water. We categorized the grid cells into four groups depending on when their open water had disappeared. Water grid cells 1 (WG 1) were grid cells that lost their open water during 1947–1965. Water grid cells 2 (WG 2) and water grid cells 3 (WG 3) were those that lost their open water during 1965–1976 and 1976–2007, respectively. Water grid cells 4 (WG 4) were grid cells that are existent until 2007. We calculated the distance to the nearest drainage ditch from the center of the WGs using ArcGIS, and also calculated the mean distance to the nearest ditch from each WG.

Vegetation survey and analysis

In order to clarify the impact of open water loss on vegetation of the mire pools, we randomly selected total 75 survey points of the persisting pools and drained area of former pools by comparing two aerial photographs (1947 and 2007) using the software ArcMap 10.1 in ArcGIS. We surveyed the vegetation on the 75 survey points (2 m × 2 m quadrat) with the phytosociological method (Braun-Blanquet 1964) in the summers of 2012 and 2013. The 75 survey points were mapped using GPS. We conducted clustering of the vegetation data for grouping plant communities, and then speculated the vegetation changes among the plant communities based on their floristic composition.

To demonstrate floristic changes among the plant communities in detail, we analyzed the vegetation data by dividing total plant species into four categories according to their plant life-forms and habitat characteristics. These categories are aqua, herb, tree, and bryo. The ‘aqua’ category refers to aquatic plants including emergent, floating-leaved, submerged, free-floating plants (Kadono 2014). The ‘herb’ category refers to herbaceous plants including herbs, grasses, and ferns except for aquatic herbaceous plants. The ‘tree’ category refers to woody plants including vines, shrubs and trees. The ‘bryo’ refers to bryophyte. Moreover, the vascular plants were also sorted into wetland or non-wetland plant species termed by Wetland plant database in Hokkaido (Suzuki et al. 2016). The nomenclature of all plant species followed the Japanese scientific name index (Y list) based on the most recent version of the Angiosperm Phylogeny Group classification (APG III) (Yonekura and Kajita 2015) for the scientific names of vascular plants and bryophytes. We calculated the mean number of species of four plant categories with the number of wetland and non-wetland plant species in each plant community.

In order to identify the impact of drainage on the plant communities, we calculated the distance to the nearest drainage ditch from the 75 survey points using ArcGIS, and also calculated the mean distance to the nearest ditch from each plant community. Using the water grid cells which include the 75 survey points, we calculated the proportion of the WGs in each plant community.

Data analysis

The Kruskal-Wallis test was used to test difference in the mean distance to the nearest ditch from each WG, and the multiple comparison test after Kruskal-Wallis was used to ascertain significance between the WGs ($p < 0.05$) using the function kruskalmc (Siegel and Castellan 1988) available in the package pgirmess (Giraudoux 2015) of the R software ver. 3.1.3 (R Core Team 2013). The original species cover-abundance values of the Braun-Blanquet scale were transformed by the 1–9 Ordinal Transform Scale (van der Maarel 1979). Cluster analysis was conducted for grouping the survey plots using a Bray-Curtis similarity measurement and flexible beta linkage (β=-0.25), and indicator species analysis was applied to calculate indicator values for all species and their significances for the plant communities. These analysis were conducted using packages cluster (Maechler et al. 2015), indicspecies (De Cáceres and Jansen 2015), vegan (Oksanen et al. 2015), and labdsv (Roberts 2015) of the R software, and all other statistical tests were also performed using R. The Kruskal-Wallis test was also used to test the difference in the mean distance to the nearest ditch from each plant community, and the multiple comparison test after Kruskal-Wallis was used to find out significances between the plant communities ($p < 0.05$).

Results

Chronological change of total length of drainage ditches and total area of open water

In the analysis of multi-temporal aerial photographs, the total length of the drainage ditches had increased over time, whereas the total area of open water had decreased (Fig. 3). There were no drainage ditches in 1947. However since the mire lost its status as the national natural monument in 1951, drainage ditches had increased rapidly to 37.3 km for the conversion of agricultural land in Period 1 (1947–1965). As a result, the total area of open water had declined remarkably from 34.28 ha to 3.87 ha. During Period 2 (1965–1976), there was less considerable change than Period 1; however, drainage ditches had been continuously dug and increased from 37.3 km to 43.71 km, and open water area had been lost from 3.87 ha to 1.7 ha. During Period 3 (1976–2007), although the total length of the drainage ditches decreased from 43.71km to 35.93km, the total area of open water had still declined from 1.7 ha to 1.02 ha marginally.

In the analysis of open water grid cells, the multiple comparison test after Kruskal-Wallis revealed that there was no significant difference in the mean distance to the nearest ditch between WG 1 and WG 2, while all other pairwise comparisons showed significant differences (Fig. 4). WG 1 and WG 2 were much closer to the drainage ditch than WG 3 and WG 4, while WG 4 was furthermost to the drainage ditch on average. The mean distance to the nearest ditch from WG 1 and WG 2 were approximately 20 m, WG 3 was approximately 46 m, and WG 4 was approximately 72 m on average.

Division of plant communities and the distance to the nearest ditch from each plant community

In the 75 survey plots, a total of 56 plant species were recorded. The plant communities were divided into four groups by clustering the vegetation data, *Nymphaea tetragona – Menyanthes trifoliata* community (*N – M*, 17 plots), *Menyanthes trifoliata – Rhynchospora alba* community (*M – R*, 13 plots), *Rhynchospora alba – Moliniopsis japonica* community (*R – M*, 25 plots), and *Moliniopsis japonica – Solidago virgaurea* subsp. *leiocarpa* community (*M – S*, 20 plots) (Table 1). The *N – M* was pool vegetation consisting mainly of Species groups A and B. This community was composed mainly of aquatic plants like *Brasenia schreberi*, *Nymphaea tetragona*, *Schoenoplectus hotarui*, *Menyanthes trifoliata*. The *M – R* was transitional vegetation between pool and drained area of former pool consisting mainly of Species groups B and C, including a few elements of Species group D. This community was composed mainly of hollow vegetation including *Rhychospora alba*, *Utricularia uliginosa*, *Juncus papillosus* and a few elements of aquatic plants. The *R – M* was weakly drained area of former pool consisting mainly of Species groups C, D, and E. This community was composed mainly of hollow and lawn vegetation. The *M – S* was more strongly drained area of former pool consisting mainly of Species groups D and E, including a few elements of Species group C. This community was composed mainly of lawn vegetation and little elements of hollow vegetation.

From the division of plant categories (Fig. 5), the *N – M* consisted mostly of aquatic plants (aqua), little herbaceous plants (herb), and a very few woody plants (tree), but all the plants were wetland plant species. The *M – R* consisted mostly of herb, little aqua, and a very few tree. This community was composed almost entirely of wetland plant species, but there were a very few non-wetland plant species in the herb. The $R - M$ consisted mostly of herb and little aqua and tree, and a very few bryophyte (bryo). This community was almost wetland plant species but a very few non-wetland plant species in the herb and tree. The $M - S$ consisted mostly of herb and tree, little aqua, and a very few bryo. This community was almost wetland plant species, but a very few non-wetland plant species in the herb and tree.

With regard to the distance to the nearest ditch from each plant community (Fig. 6), the $N - M$ was farther away from drainage ditches, whereas the other three plant communities ($M - R$, $R - M$, and $M - S$) associated with drained area of former pool were closer to drainage ditches. There were significant differences between the distance to the nearest ditch from $N - M$ and those from $M - R$, $R - M$, and $M - S$, but there were no significant differences between the distances to the nearest ditch from $M - R$, $R - M$, and $M - S$.

With regard to the proportion of WGs which include the survey points in each plant community (Fig. 7), the survey points of $N - M$ (17 points) were included only in WG 4. The 3, 6, 3, 1 survey points of $M - R$ (13 points) were included in WG 1, WG 2, WG 3, and WG 4, respectively. The 16, 5, 4 survey points of $R - M$ (25 points) were included in WG 1, WG 2, and WG 3, respectively. The 8, 9, 2, 1 survey points of $M - S$ (20 points) were included in WG 1, WG 2, WG 3, and WG 4, respectively.

Discussion

Open water shrinkage of mire pools caused by drainage ditches

Fens and bogs, and mire pools formed in peatlands were destroyed by agriculture and large-scale national projects undertaken during the latter 20th century in many countries; pool ecosystems have been damaged seriously by various human activities (National Research Council 1992; Verhoeven et al. 1996; Mitsch and Gosselink 2015). Our result shows the fact that many mire pools have artificially disappeared by a fast development for agriculture. There were striking increases of drainage ditches during Period 1 and Period 2, whereas there were absolutely no drainage ditches before Period 1 (Fig. 3). This is supposed that the open water of the mire pools declined remarkably until 1970s in Shizukari Mire. In Hokkaido, extensive agricultural development and urbanization have progressed following World War II (Nakamura and Yamada 2005).

Notably in the west and central parts of Hokkaido including the Shizukari Mire, losses of wetlands were severe between the 1950s and 1970s (Fujita et al. 2009).

Drainage was caused by ditches dug during Period 1 and Period 2 (Fig. 3), and the open water lost during Period 1 and Period 2 (WG 1 and WG 2) were approximately 20 m distant to the nearest ditch (Fig. 4). Our interpretation is that most of the loss of mire pools in the Shizukari Mire took place soon after digging of ditches. Several Canadian studies that looked at the effects of ditching on lowering the water table in peatlands have suggested that drainage is most effective within ten to 15 m of a ditch (Tóth and Gillard 1988; Belleau et al. 1992; Roy et al. 2000). Moreover, most of the drying effect associated with a drainage ditch in bogs usually occurs within 25m (Hillman 1992; Rothwell et al. 1996).

However, depending on the composition and the structure of the peat, the drainage ditches can impact great distances from drainage installations (Landry and Rochefort 2012). It should be noted that during Period 3 despite decline of total length of drainage ditches due to aging and lack of maintenance of the ditches, open water area had been slightly decreased continuously (Fig. 3). In addition, the open water lost during Period 3 and existing open water (WG 3 and WG 4) were on average 46 m and 72 m distant to the nearest ditch, respectively (Fig. 4). Boelter (1972) concluded that if the peat is fibric, the water table more than 50 m away from a drainage ditch can be lowered. Moreover, drainage is a source of cumulative environmental change because of its repetitive and expansive nature (Spaling and Smit 1995). The cumulative nature of drainage is apparent in increasing drainage density over time (Spaling and Smit 1995). These suggest that remaining open water in the mire pools could shrink continuously due to existing drainage ditches if protections are not implemented.

Our results indicate that immediate drainage from near the ditch by digging ditches is most effective for the water table less than 20 m away from the drainage ditches in short-term, and moreover, water table more than 50 m away from the drainage ditches is also lowered by continued drainage effect in longer-term. In conclusion, digging ditches not only cause immediate drainage but also continued drainage effect.

Vegetation change of pool plant communities caused by open water loss

From our results, we could suppose the sequence of vegetation change of pool plant community. It is suggested that open water loss caused the vegetation change mainly from the pool plant communities (*N* – *M*) to the plant communities of drained area of former pools (*M* – *R*, *R* – *M*, and finally to *M* – *S*). The aquatic plants were lost, and wetland plant species except the aquatic plants drastically increased from $N-M$ to $M-R$, $R-M$, but declined from $R-M$ to $M-S$ (Fig. 5). It is considered that wetland plant species could occupy and increased in the area because the drained area of former pool remained under wet condition. However, as the drainage effect continued, the woody plants gradually increased and non-wetland plant species also appeared from $M-R$ to $R-M$ and $M-S$ (Fig. 5). It is considered that intensifying drainage caused the occurrence of woody plants and decline of wetland plant species of herbaceous plants. Lowered water table due to drainage results in vegetation typical of drier conditions than natural (Howie et al. 2009). The plant species living on wet surfaces are the first to disappear, while hummock-dwelling species (e.g. dwarf shrubs) may even benefit from drainage (Sarasto 1961; Eurola et al. 1984).

In our interpretation, this change from $N-M$ to $M-R$, $R-M$, and finally to $M-S$ was more likely the closer to a drainage ditch (Fig. 6). In particular, $R-M$ and $M-S$, which are characterized by disappearance of aquatic plants except for *Phragmites australis* and invasion of woody plants, were even nearer to the drainage ditch than others. On the other hand, the plant community of persisting pools ($N-M$) was farther than any other communities of drained area of former pools ($M-R$, $R-M$, and $M-S$) (Fig. 6). These results indicate that the drier soil resulting from lower water tables following drainage has brought about distinct changes in the types of vegetation and the land in the immediate vicinity of ditches is more effectively drained than land some distance away (Frolik 1941). This differential efficiency in drainage brings about zonation in the vegetation on the various parts of a drained area, the more advanced stages lying in closer proximity to the ditches (Frolik 1941).

However, the pool plant community does not necessarily change in the sequence from $N-M$ to $M-R$, $R-M$, and $M-S$. There were not significant differences among the distances to the nearest ditch from the plant communities of drained area of former pools ($M-R$, $R-M$, and $M-S$) (Fig. 6). In addition, there were no large differences in the proportions of WGs which include the points of vegetation survey among the $M-R$, $R-M$, and $M-S$, although the proportions of WG 1 and WG 2 were very large (Fig. 7). These results indicate that the rate of vegetation change may be different, because the rate of drainage is different depending on the composition and the structure of the peat soil.

Our results about vegetation change also suggest that, without any protections, the vegetation change towards woody vegetation and loss of aquatic vegetation could be continued, because most plant communities associated with the mire pools including the drained area of former pools are located less than 100 m away from the drainage ditches

(Fig. 6). Some previous studies said that effects of drainage on bog water table, and indirect effects on vegetation communities are rarely perceptible at distances exceeding 100 m away from a ditch (Hillman 1992; Poulin et al. 1999; Roy et al. 2000). In other words, effects of drainage on vegetation communities can be influential at distances less than 100 m away from a ditch.

Conclusions

This study identified the effects of drainage on open-water mire pools. Most open water of mire pools was lost soon after digging of ditches. Moreover, remaining open water also has shrunk by more diffuse, continued drainage effect. The open water loss caused the vegetation change of pool plant communities. These results were related to the distance from the ditch. The closer to the drainage ditch, these changes became severer.

This study might be the first study focusing on not only the surface hydrological dynamics of open water of the mire pools affected by drainage but also on the vegetation change of the mire pools. We demonstrated a negative effect of drainage and realized that we must protect the remaining mire and mire pools from drainage in any way. If the remaining mire pools disappear due to continued drainage effect, the mire vegetation will become more homogenous and the mire will lose its function as the mire ecosystem. Although restoration of disappeared mire pools is important, it is more significant to preserve the remaining mire pools from continued drainage effect.

Acknowledgements

This study was financially supported by the Environment Research and Technology Development Fund (S9) of the Ministry of the Environment, Japan (http://s9.conservationecology.asia). We thank gratefully for support of the Ministry of the Environment.

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Table 1 The species composition of four plant communities. Plant communities are named as *Nymphaea tetragona* – *Menyanthes trifoliata* community (*N* – *M*), *Menyanthes trifoliata* – *Rhynchospora alba* community (*M* – *R*), *Rhynchospora alba* – *Moliniopsis japonica* community (*R* – *M*), and *Moliniopsis japonica* – *Solidago virgaurea* subsp. *leiocarpa* community (*M* – *S*).

plant community			***N* − *M***	***M* − *R***	***R* − *M***	***M* − *S***
the total number of survey plot			17	13	25	20
the mean number of species / survey plot			5	9	15	13
Division of plant species	Family name	Species name	Frequency of plant species in each plant community			
		Species group A				
aqua/wet	Lentibulariaceae	*Utricularia japonica*	Ⅱ$_{+\text{-}5}^{***}$	-	-	-
aqua/wet	Cabombaceae	*Brasenia schreberi*	Ⅲ$_{+\text{-}4}^{***}$	-	-	-
aqua/wet	Nymphaeaceae	*Nymphaea tetragona*	Ⅳ$_{+\text{-}4}^{***}$	Ⅰ$_{1}$	-	-
aqua/wet	Cyperaceae	*Schoenoplectus hotarui*	Ⅳ$_{+\text{-}2}^{***}$	Ⅰ$_{1}$	-	-
		Species group B				
aqua/wet	Menyanthaceae	*Menyanthes trifoliata*	Ⅳ$_{+\text{-}3}^{**}$	Ⅳ$_{+\text{-}2}$	Ⅰ$_{+}$	-
herb/wet	Iridaceae	*Iris laevigata*	Ⅲ$_{+\text{-}3}$	Ⅲ$_{+\text{-}1}$	Ⅳ$_{+\text{-}1}$	Ⅰ$_{+\text{-}1}$
		Species group C				
herb/wet	Cyperaceae	*Rhynchospora alba*	Ⅰ$_{+}$	Ⅴ$_{3\text{-}4}^{***}$	Ⅴ$_{1\text{-}4}$	Ⅱ$_{+\text{-}1}$

herb/wet	Lentibulariaceae	*Utricularia uliginosa*	I $_{+-1}$	V $_{+-1}^{***}$	Ⅳ $_{+-1}$	I $_{+}$
herb/wet	Cyperaceae	*Rhynchospora fauriei*	I $_{+}$	Ⅳ $_{+-1}$	Ⅳ $_{+-4}^{*}$	Ⅱ $_{+-1}$
herb/wet	Juncaceae	*Juncus papillosus*	-	V $_{1-2}^{***}$	V $_{+-2}$	Ⅱ $_{+-1}$
herb/wet	Orchidaceae	*Pogonia japonica*	-	Ⅳ $_{+-1}^{**}$	Ⅳ $_{+-1}$	Ⅱ $_{+}$
herb/wet	Droseraceae	*Drosera rotundifolia*	-	Ⅲ $_{+-1}$	V $_{+-3}^{***}$	Ⅲ $_{+-1}$
herb/wet	Orchidaceae	*Platanthera tipuloides* subsp. *nipponica*	-	Ⅱ $_{+-1}$	Ⅲ $_{+-1}^{**}$	I $_{+}$
herb/non	Haloragaceae	*Haloragis micrantha*	-	I $_{+}$	Ⅲ $_{+-1}^{**}$	Ⅱ $_{+-1}$
		Species group D				
herb/wet	Poaceae	*Moliniopsis japonica*	I $_{+}$	Ⅱ $_{+-2}$	V $_{+-3}$	V $_{+-4}^{***}$
tree/wet	Ericaceae	*Vaccinium oxycoccos*	I $_{+}$	I $_{+}$	Ⅱ $_{+-1}$	Ⅲ $_{+}^{**}$
herb/wet	Cyperaceae	*Carex middendorffii*	-	Ⅱ $_{+-1}$	I $_{1-4}$	Ⅳ $_{+-3}^{***}$
tree/wet	Myricaceae	*Myrica gale* var. *tomentosa*	-	I $_{+}$	Ⅳ $_{+-2}$	V $_{1-3}^{***}$
herb/wet	Rosaceae	*Sanguisorba tenuifolia*	-	I $_{+}$	Ⅳ $_{+}$	V $_{+-1}^{***}$
		Species group E		-		
herb/wet	Violaceae	*Viola verecunda* var. *semilunaris*	-	-	Ⅳ $_{+-1}^{***}$	Ⅲ $_{+}$
herb/wet	Campanulaceae	*Lobelia sessilifolia*	-	-	Ⅳ $_{+-2}^{***}$	Ⅱ $_{+-1}$
herb/wet	Asteraceae	*Solidago virgaurea* subsp. *leiocarpa*	-	-	Ⅲ $_{+}$	V $_{+-1}^{***}$
tree/wet	Aquifoliaceae	*Ilex crenata* var. *radicans*	-	-	Ⅱ $_{+-1}$	Ⅲ $_{+-5}^{***}$
tree/wet	Hydrangeaceae	*Hydrangea paniculata*	-	I $_{+}$	I $_{+}$	Ⅲ $_{+-2}^{***}$
		Others		-		
aqua/wet	Poaceae	*Phragmites australis*	V $_{+-2}$	V $_{+-2}$	V $_{+-3}$	V $_{+-3}$
tree/wet	Betulaceae	*Alnus japonica*	-	-	-	I $_{+}$
aqua/wet	Cyperaceae	*Eleocharis congesta*	I $_{+}$	-	I $_{+}$	-
herb/wet	Cyperaceae	*Carex limosa*	I $_{+-2}$	I $_{1}$	I $_{1}$	-
herb/wet	Lycopodiaceae	*Lycopodium inundatum*	I $_{+}$	I $_{1}$	Ⅱ $_{+-2}^{*}$	I $_{+}$
tree/non	Taxaceae	*Taxus cuspidata*	-	-	I $_{+}$	-
herb/wet	Celastraceae	*Parnassia palustris* var. *palustris*	-	-	Ⅱ $_{+-1}^{*}$	I $_{+-1}$
herb/wet	Orchidaceae	*Epipactis thunbergii*	-	-	I $_{+}$	I $_{1}$
tree/wet	Ericaceae	*Ledum palustre* subsp. *diversipilosum* var. *diversipilosum*	-	-	-	I $_{+}$
herb/wet	Primulaceae	*Lysimachia vulgaris* var. *davurica*	-	-	-	I $_{+}$
herb/wet	Cyperaceae	*Eleocharis wichurae*	-	-	-	I $_{1}$
herb/non	Poaceae	*Miscanthus sinensis*	-	-	I $_{+}$	I $_{1}$
herb/wet	Asparagaceae	*Hosta sieboldii* var. *rectifolia*	-	-	I $_{+}$	I $_{+-1}$
tree/non	Anacardiaceae	*Toxicodendron radicans* subsp. *orientale*	-	-	I $_{+}$	I $_{+}$

herb/wet	Thelypteridaceae	*Thelypteris nipponica*	-	-	-	I $_{+\text{-}1}$
herb/wet	Orchidaceae	*Spiranthes sinensis* var. *amoena*	-	-	I $_{+}$	-
herb/wet	Thelypteridaceae	*Thelypteris palustris*	-	-	-	I $_{+}$
tree/wet	Ericaceae	*Andromeda polifolia*	-	-	-	I $_{+}$
herb/wet	Lamiaceae	*Lycopus maackianus*	-	-	I $_{+\text{-}1}$	I $_{+}$
herb/non	Asteraceae	*Eupatorium makinoi*	-	-	I $_{+}$	-
herb/wet	Scheuchzeriaceae	*Scheuchzeria palustris*	-	-	-	I $_{+}$
herb/wet	Gentianaceae	*Gentiana triflora* var. *japonica*	-	-	II $_{+}^{*}$	I $_{+}$
herb/wet	Hypericaceae	*Triadenum japonicum*	-	-	I $_{+}$	I $_{+\text{-}1}$
herb/wet	Cyperaceae	*Carex michauxiana* subsp. *asiatica*	-	-	I $_{1}$	I $_{2}$
tree/wet	Ericaceae	*Chamaedaphne calyculata*	-	-	-	I $_{+\text{-}1}$
tree/non	Anacardiaceae	*Toxicodendron trichocarpum*	-	-	-	II $_{+\text{-}3}^{***}$
herb/wet	Osmundaceae	*Osmunda cinnamomea* subsp. *asiatica*	-	-	I $_{+}$	II $_{+\text{-}3}^{**}$
herb/wet	Cyperaceae	*Eriophorum vaginatum* subsp. *fauriei*	-	-	I $_{+\text{-}1}$	I $_{+\text{-}1}$
herb/wet	Dennstaedtiaceae	*Pteridium aquilinum* subsp. *japonicum*	-	-	-	I $_{+\text{-}2}$
bryo/spha	Sphagnaceae	*Sphagnum papillosum*	-	-	-	I $_{5}$
bryo/spha	Sphagnaceae	*Sphagnum compactum*	-	-	I $_{3}$	-
bryo/moss	Hypnaceae	*Callicladium haldanianum*	-	-	-	I $_{1}$

Significances of indicator species are marked with asterisks : *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, Frequency of species in each plant community: I (sparse) = 1–20%, II (occasional) = 21–40%, III (frequent) = 41–60%, IV (constant) = 61–80%, V (constant) = 81–100%, Braun-Blanquet's cover-abundance scale: + = a few individuals (< 10%), 1 = numerous individuals (< 10%), 2 = 10–25%, 3 = 25–50%, 4 = 50–75%, 5 = 75–100%.

Figure Captions

Fig. 1 Location of the study area (Shizukari Mire in Hokkaido Island, Northern Japan).

Fig. 2 The ranges of Shizukari Mire. (a) the mire area in 1917 (pristine mire) and in 1996 (remaining mire) and the analysis ranges of multi-temporal aerial photographs and vegetation survey, (b) the analysis range of multi-temporal aerial photographs in aerial photo of 1947, (c) the range of remaining mire in aerial photo of 2007 (a: Digital Topographic Map (Tile) published by Geospatial Information Authority of Japan; the lines after Fujita and Tachibana (1998), b and c: 1947 and 2007 aerial orthophotographs authorized by Geospatial Information Authority of Japan).

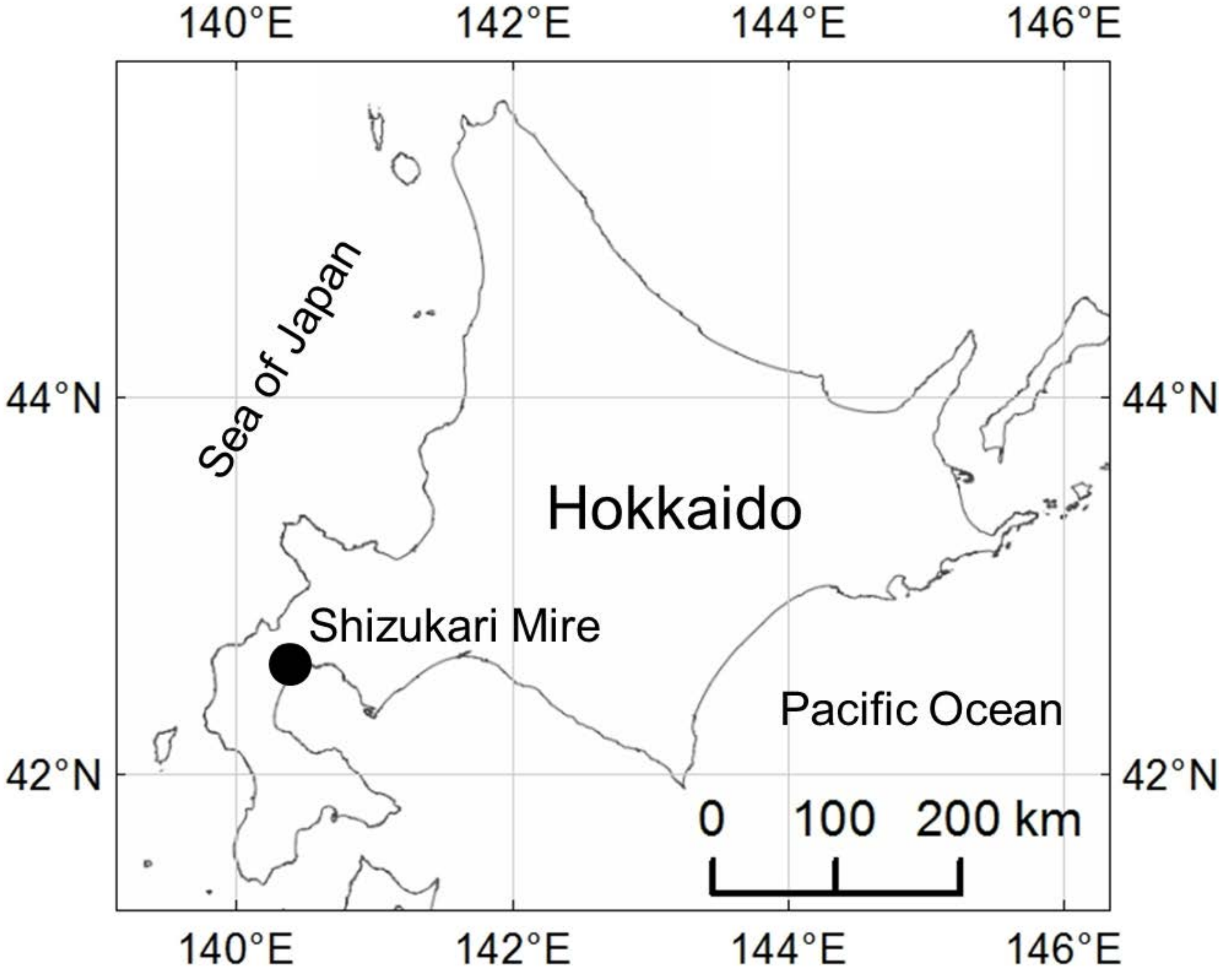
Fig. 3 Chronological change of total length of drainage ditches and total area of open water (Period 1: 1947–1965, Period 2: 1965–1976, Period 3: 1976–2007).

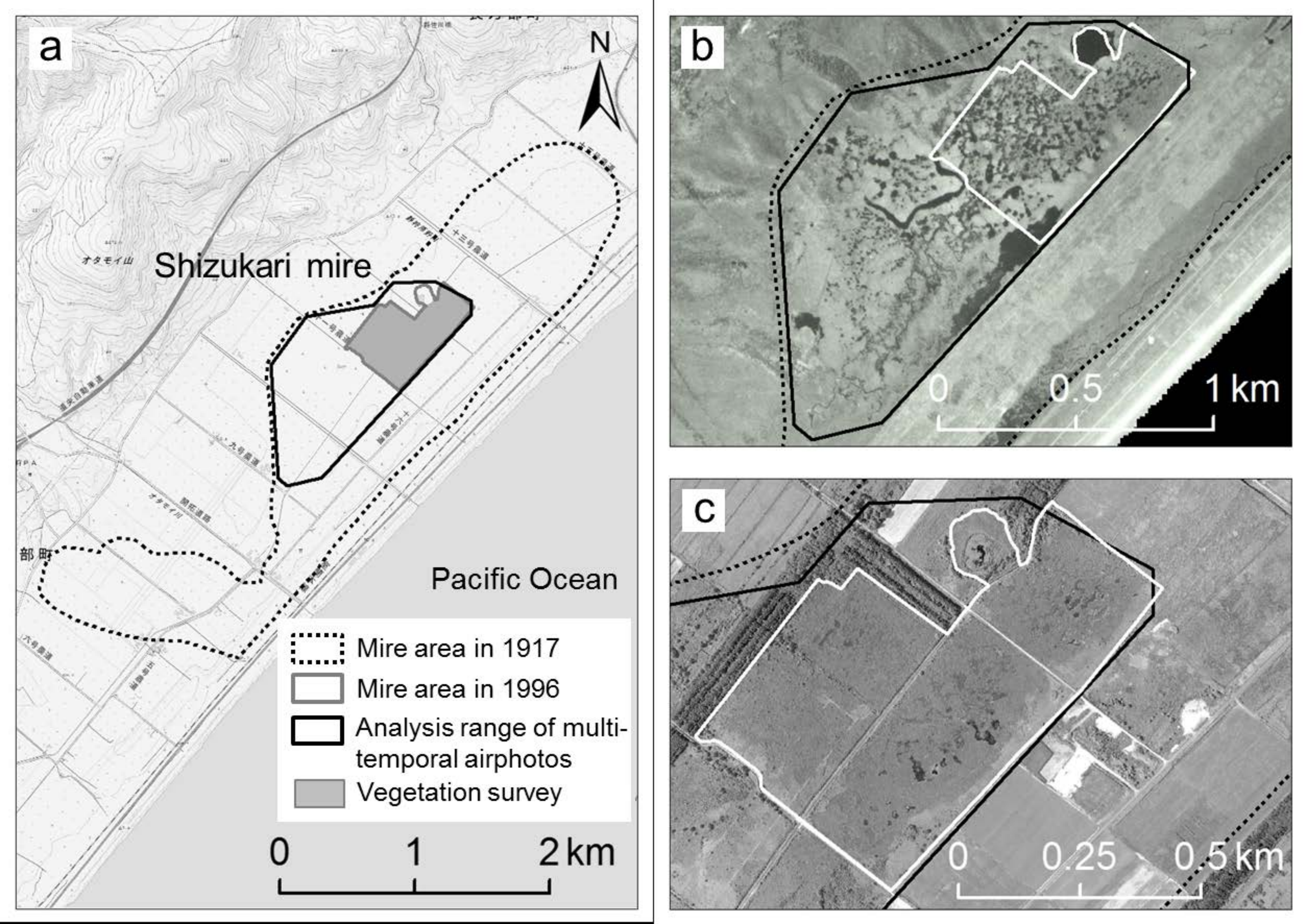
Fig. 4 The distance to the nearest drainage ditch from each group of water grid cells (WG) (WG 1: grid cells that lost open water during 1947–1965, WG 2: grid cells that lost open water during 1965–1976, WG 3: grid cells that lost open water during 1976–2007, WG 4: grid cells that are still existing in 2007). Different letters (a, b, c) indicate significant differences between the groups of water grid cells (WGs) ($p < 0.05$).

Fig. 5 Plant composition of plant communities divided into four plant categories with division of wetland plant species or non-wetland plant species (aqua: category of aquatic plants including floating, floating leaved, and emergent plants, herb: category of herbaceous plants including herbs, grasses, and ferns except for aquatic herbaceous plants, tree: category of woody plants including shrubs, vines, and trees, bryo: category of bryophyte). (a) *Nymphaea tetragona – Menyanthes trifoliata* community (*N – M*), (b) *Menyanthes trifoliata – Rhynchospora alba* community (*M – R*), (c) *Rhynchospora alba – Moliniopsis japonica* community (*R – M*), and (d) *Moliniopsis japonica – Solidago virgaurea* subsp. *leiocarpa* community (*M – S*).

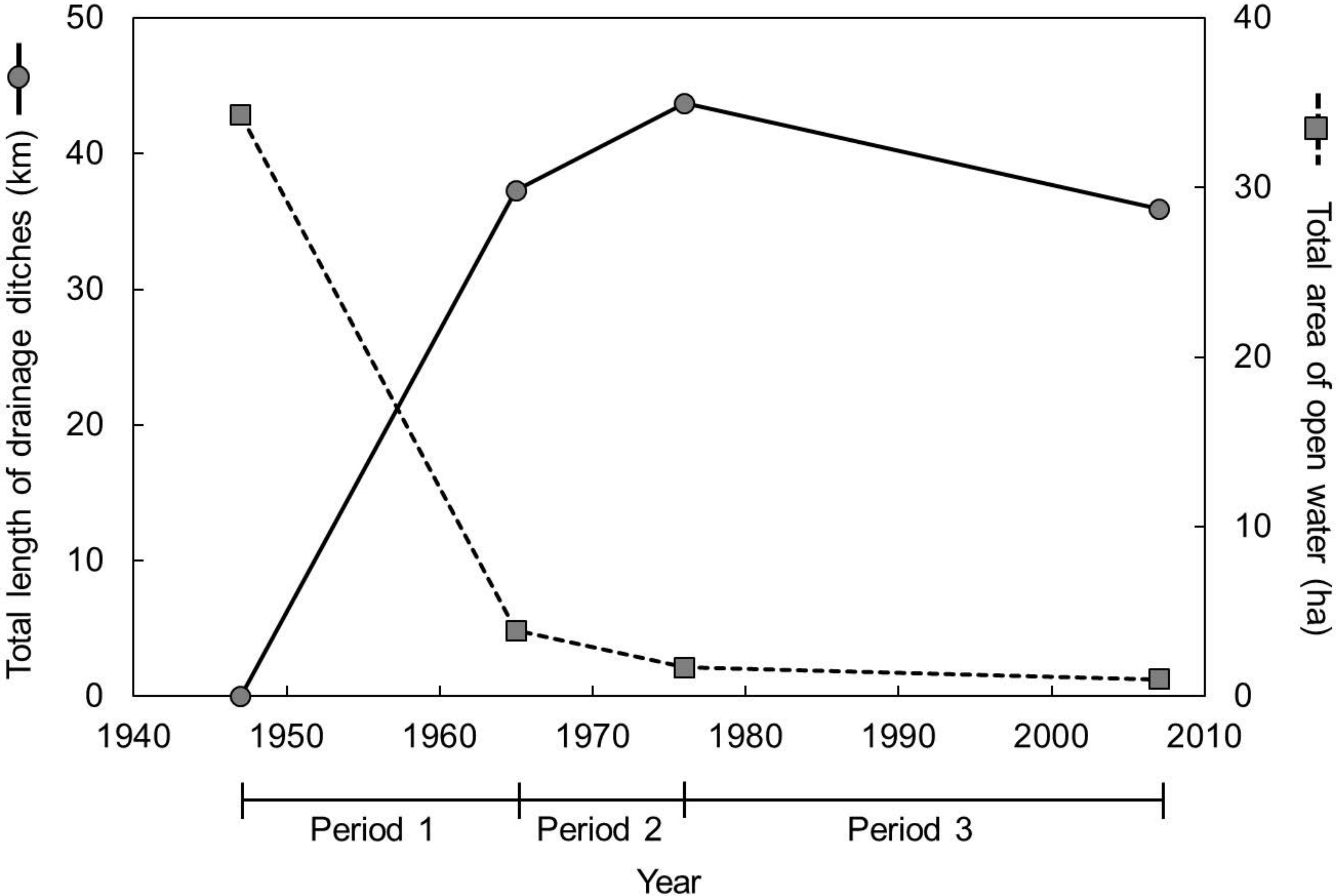
Fig. 6 The distance to the nearest drainage ditch from each plant community (*N – M*: *Nymphaea tetragona – Menyanthes trifoliata* community, *M – R*: *Menyanthes trifoliata – Rhynchospora alba* community, *R – M*: *Rhynchospora alba – Moliniopsis japonica community*, *M – S*: *Moliniopsis japonica – Solidago virgaurea* subsp. *leiocarpa community*). Different letters (a, b) indicate significant differences between the plant communities ($p < 0.05$).

Fig. 7 The proportion of WGs which include the survey points in each plant community (*N – M*: *Nymphaea tetragona – Menyanthes trifoliata* community, *M – R*: *Menyanthes trifoliata – Rhynchospora alba* community, *R – M*: *Rhynchospora alba – Moliniopsis japonica community*, *M – S*: *Moliniopsis japonica – Solidago virgaurea* subsp. *leiocarpa community*; WG 1: grid cells that lost open water during 1947–1965, WG 2: grid cells that lost open water during 1965–1976, WG 3: grid cells that lost open water during 1976–2007, WG 4: grid cells that are still existing in 2007).

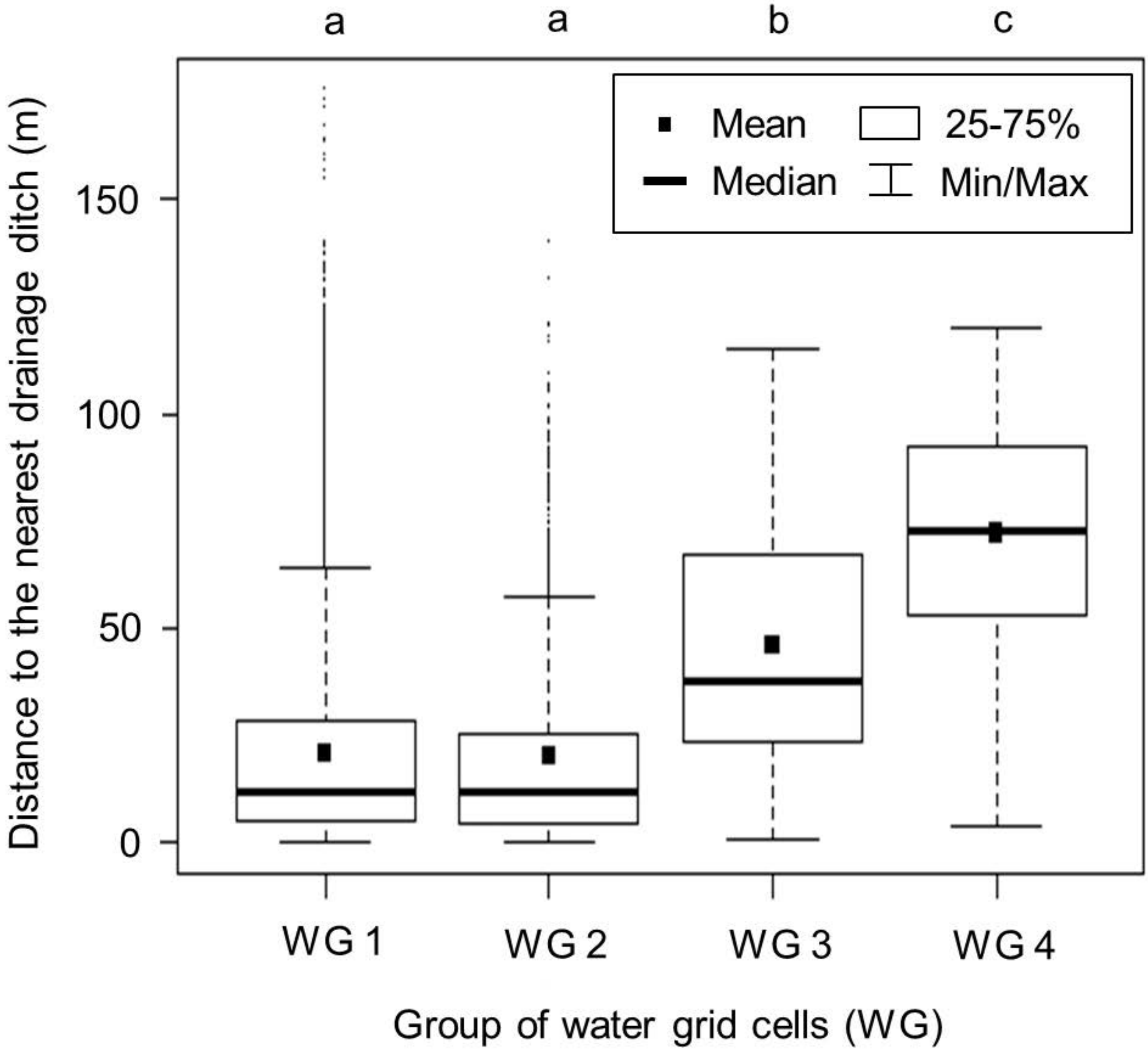

140°E
142°E
144°E
146°E
44°N
42°N
Sea of Japan
Hokkaido
Shizukari Mire
Pacific Ocean
0
100
200 km



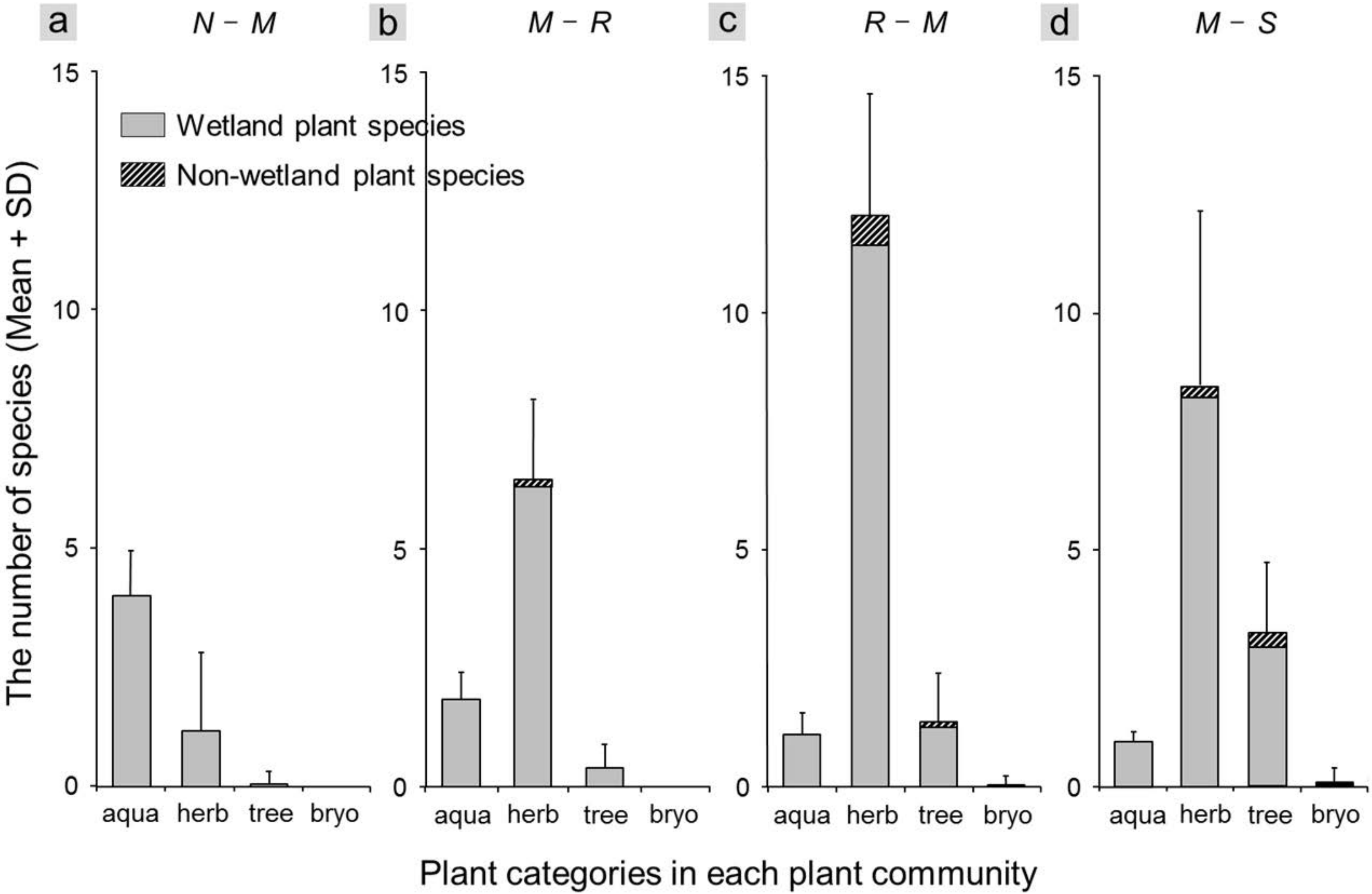
a
N
Shizukari mire
Pacific Ocean
Mire area in 1917
Mire area in 1996
Analysis range of multi-temporal airphotos
Vegetation survey
0
1
2 km
b
0
0.5
1 km
c
0
0.25
0.5 km

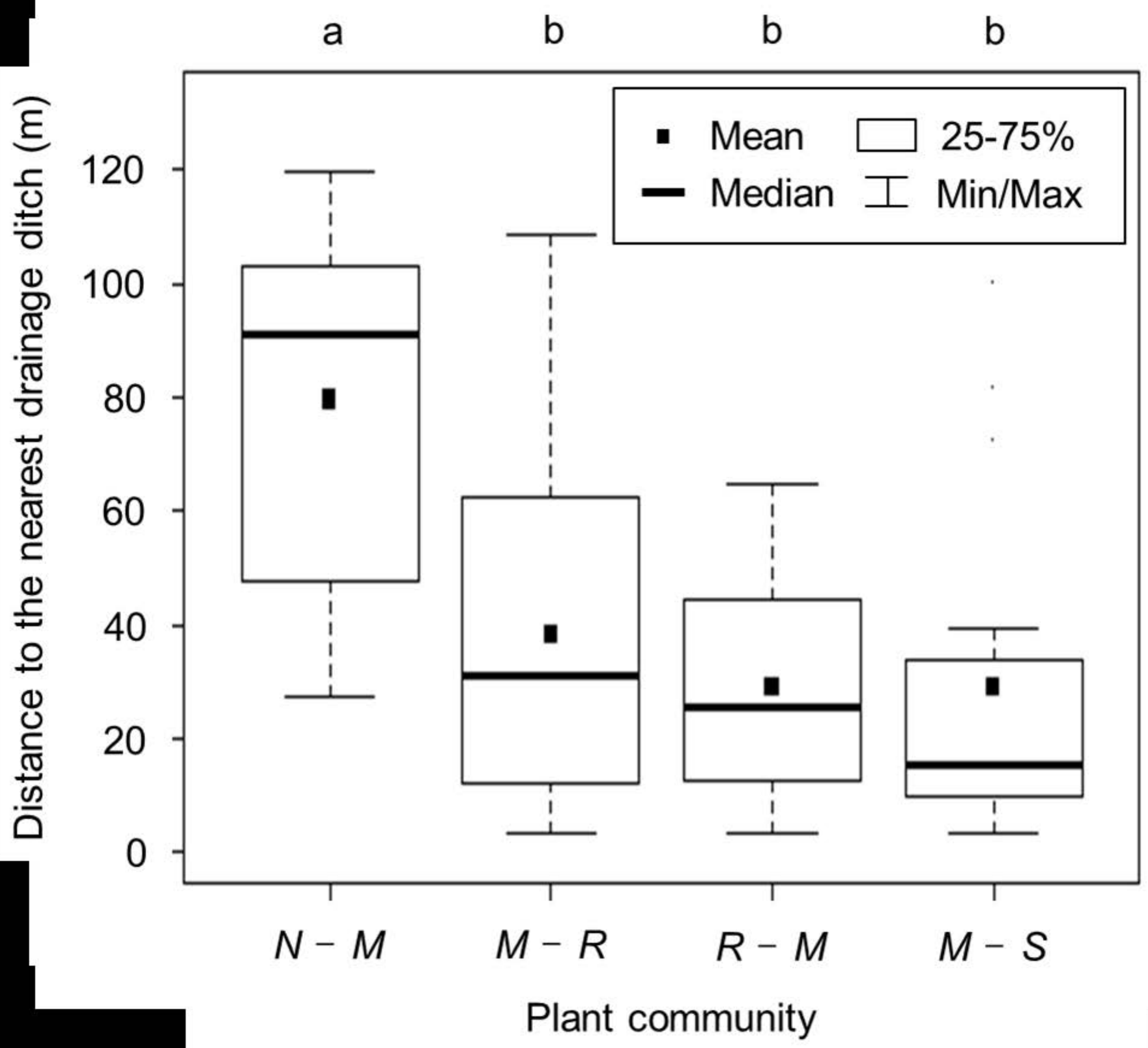


Total length of drainage ditches (km)
Total area of open water (ha)
50
40
30
20
10
0
40
30
20
10
0
1940
1950
1960
1970
1980
1990
2000
2010
Period 1
Period 2
Period 3
Year

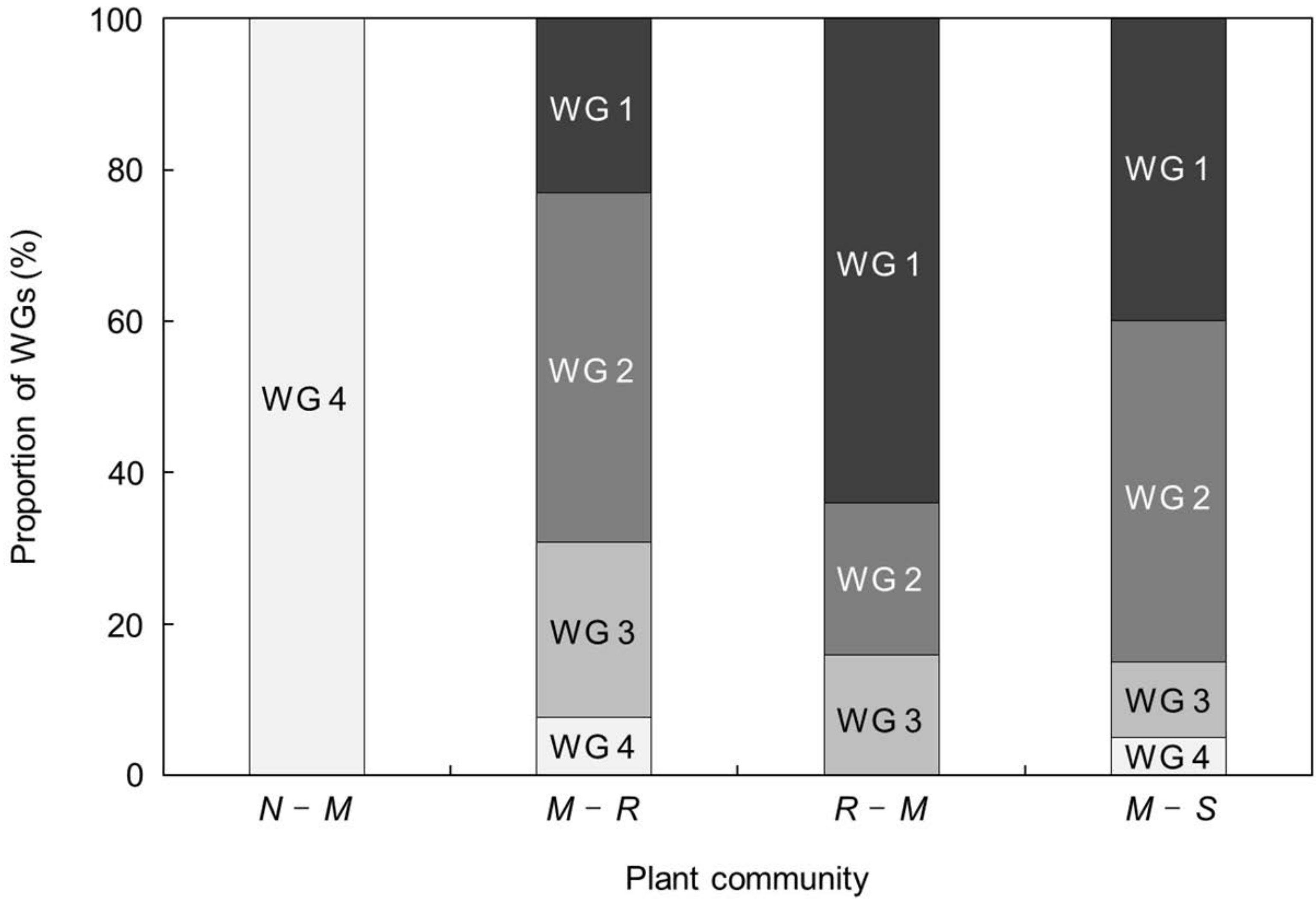


a
a
b
c
Mean
25-75%
Median
Min/Max
Distance to the nearest drainage ditch (m)
150
100
50
0
WG 1
WG 2
WG 3
WG 4
Group of water grid cells (WG)


a
N – M
b
M – R
c
R – M
d
M – S
Wetland plant species
Non-wetland plant species
The number of species (Mean + SD)
15
10
5
0
aqua
herb
tree
bryo
Plant categories in each plant community



a
b
b
b
Mean
25-75%
Median
Min/Max
Distance to the nearest drainage ditch (m)
0
20
40
60
80
100
120
N – M
M – R
R – M
M – S
Plant community



100
80
60
40
20
0
Proportion of WGs (%)
WG 4
WG 1
WG 2
WG 3
WG 4
WG 1
WG 2
WG 3
WG 1
WG 2
WG 3
WG 4
N − M
M − R
R − M
M − S
Plant community