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Fire disturbance promotes biodiversity of plants, lichens and birds in the Siberian subarctic tundra

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Abstract

Fire shapes the world's terrestrial ecosystems and has been influencing biodiversity patterns for millennia. Anthropogenic drivers alter fire regimes. Wildfires can amplify changes in the structure, biodiversity and functioning of the fast-warming tundra ecosystem. However, there is little evidence available, how these fires affect species diversity and community composition of tundra ecosystems over the long term. We studied long-term fire effects on community composition and diversity at different trophic levels of the food web in the subarctic tundra of Western Siberia. In a space-for-time approach we compared three large fire scars (>44, 28 and 12 years old) to unburnt controls. We found that diversity (measured as species richness, Shannon index and evenness) of vascular and non-vascular plants and birds was strongly affected by fire, with the greatest species richness of plants and birds for the intermediate-age fire scar (28 years). Species composition of plants and birds still differed from that of the control >44 years after fire. Increased deciduous shrub cover was related to species richness of all plants in a hump-shaped manner. The proportion of southern (taiga) bird species was highest in the oldest fire scar, which had the highest shrub cover. We conclude that tundra fires have long-term legacies with regard to species diversity and community composition. They may also increase landscape-scale species richness and facilitate range expansions of more southerly distributed species to the subarctic tundra ecosystem.

KEYWORDS
birds, bryophytes, indicator species, lichens, plants, Russia, self-organizing map, shrub cover

1 | INTRODUCTION

Fire is an important ecological and evolutionary force that has shaped the world's terrestrial ecosystems for millennia, strongly influencing biodiversity patterns in fire-prone landscapes (He et al., 2019); however, fire regimes are being altered by anthropogenic drivers, leading to modifications in ecosystem composition (Kelly et al., 2020). Arctic and subarctic ecosystems experience wildfire events less often than other biomes (Archibald et al., 2013; Viereck & Schandelmeier, 1980), but climate change is expected to increase fire frequency and extent at high latitudes (Hu et al., 2015; Moskovchenko et al., 2020).

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Wildfires can amplify climate change-induced processes in tundra ecosystems (Hu et al., 2015; Pachauri et al., 2014), including shifts in ecosystem structure, biodiversity and ecosystem functioning (Berner et al., 2020; Bjorkman et al., 2020; Chapin & Díaz, 2020). Species ranges shift northwards (Elmhagen et al., 2015; Wheeler et al., 2018), and northerly distributed species show range retractions and might go extinct (Chapin III et al., 1995; Meltofte et al., 2013). Such range shifts may temporarily increase species diversity in tundra ecosystems by allowing southern species to colonize more northern areas (Walker et al., 2001).

Fires often increase ecosystem productivity in tundra ecosystems (DeMarco et al., 2014; Heim et al., 2021) as they lead to increased surface soil temperature (Chambers et al., 2005; Jiang et al., 2015). Increased temperature promotes mineralization rates and permafrost thaw, leading to higher nutrient availability for plants and especially for shrubs that can reach deeper soil layers (Jansson & Hofmockel, 2020; Oulehle et al., 2016; Salmon et al., 2016). Furthermore, the disturbance through fire opens up areas where shrubs can easily establish and thus increases the reproduction rate of shrubs (Lantz et al., 2010; Myers-Smith et al., 2011; Shevtsova et al., 2020). Thus, shrub encroachment after fires can lead to significant shifts in the composition of plant communities (Myers-Smith et al., 2019). These can in turn affect bird communities (Smith et al., 2020).

After fire, species performance (i.e. how a species can use resources) as well as other biotic and abiotic factors (Chen et al., 2021; Heinken, 1999; Hylander & Johnson, 2010) strongly influence the rate at which the vegetation recovers. The vegetation development after fire substantially affects higher trophic levels, because the recovery rate of many plant species is linked to pre-fire abiotic factors at lower trophic levels (Kozlowski, 2012; Pérez et al., 2018). After a fire, vegetation patterns influence habitat conditions for many animal species through changes in microclimate (Weller & Holmgren, 1974), nesting structures and food supply (Joly et al., 2016; Kozlowski, 2012). In the subarctic tundra, shrubs are a key structure, mediating arthropod communities and therefore also breeding bird abundance and diversity (Davis et al., 2021; Ims & Henden, 2012; Kozlowski, 2012; Smith et al., 2020; Sokolov et al., 2012).

Despite a recent increase in studies investigating tundra fire dynamics (e.g. Hollingsworth et al., 2021; Klupar et al., 2021) there is a considerable gap in knowledge regarding how long-term post-fire succession shapes the diversity and composition of plant and animal communities in tundra ecosystems. Yet, this knowledge is especially important because biodiversity at high latitudes is generally understudied (Meltofte et al., 2013; Pérez et al., 2018; Sokolov et al., 2012).

Although specific knowledge on tundra post-fire recovery dynamics is scarce, related hypotheses may hint at how this could unfold. The intermediate disturbance hypothesis postulates that species diversity is highest at intermediate levels of disturbance due to the coexistence of early and late successional species (Connell, 1978) yet, it is subject to scientific controversy (e.g. Fox, 2013). This hypothesis was recently considered for fire severity in tundra ecosystems: Species diversity in plants and birds was found to be highest in areas intermediately disturbed by tundra fires (Pérez et al., 2018; Tsuyuzaki et al., 2018). Similarly, plant species diversity of tundra vegetation was found to be lowest shortly after fire and to increase with time since a fire (Frost et al., 2020; Jandt & Meyers, 2000). Therefore, the second prediction of this hypothesis, stating that species richness is highest at intermediate times after a disturbance (Collins et al., 1995), may also be expected for post-fire patterns in tundra ecosystems. However, due to the lack of long-term studies, so far almost no empirical evidence exists for this assumption.

The pyrodiversity–biodiversity hypothesis (Jones & Tingley, 2021) relates diversity patterns to the landscape scale, as it assumes that multiple spatiotemporal fire characteristics promote a heterogeneous landscape with patches of different successional age and, thereby, positively influence biodiversity at the landscape scale (He et al., 2019). Although some studies have investigated post-fire diversity patterns in relation to fire characteristics (e.g. Frost et al., 2020; Tsuyuzaki et al., 2018), very few studies have assessed the impacts of fire on biodiversity at the landscape level. From Afroalpine heathlands, for example, it is known that a fire-induced landscape mosaic can lead to species rich communities and increase their resilience to warming (Hylander et al., 2021; Johansson et al., 2018).

Here, we present a comprehensive study on long-term fire effects at the landscape level on community composition and diversity patterns of birds and plants in a tundra ecosystem. We used a space-for-time approach surveying three large fire scars (>44, 28 and 12 years old) and corresponding control areas. For the studied ecosystem, we anticipated the following outcomes:

1. Alpha diversity follows the intermediate disturbance hypothesis over decades of post-fire vegetation succession.
2. Alpha diversity of plants decreases with increasing deciduous shrub cover.
3. The proportion of southern (taiga) bird species is highest at fire scars with high shrub cover.
4. Multiple fire scars of different ages temporarily increase biodiversity at the landscape scale.
5. Even after >44 years, plant and bird species composition still differ from pre-fire conditions.

2 | MATERIAL AND METHODS

2.1 | Study area

We conducted our study in Western Siberia within the Yamalo-Nenets Autonomous Okrug (Region) between the rivers Pur and Taz. Our study area (centre at 67° 1'19.59"N, 79° 1'53.53"E, total study area size ca. 70 km^2 (Heim et al., 2021) was situated north of the Arctic Circle in the forest tundra ecozone at its northernmost border. This region has a subarctic climate growing season lasting from mid-June to early September (mean annual temperature: −8.1°C, mean January temperature: −26.2°C, mean July temperature: 14.4°C, annual precipitation: 482 mm) (Kazakov, 2019, Figure S1).

At the transition between the forest tundra to the south and the shrub tundra to the north (Yurkovskaya, 2011), the largely open landscape is sparsely dotted with larch trees (*Larix sibirica*). In comparison with other tundra areas, the landscape is rather dry and well drained with the exception of depressions and small streams. The vegetation is dominated by reindeer lichens (*Cladonia* subgenus *Cladina* spp.) that cover ~70% of the surface. Shrubs such as *Betula nana* (~25% cover) and dwarf shrubs such as *Vaccinium uliginosum* (~10% cover) are abundant, while herbs and graminoids as well as bryophytes play a subordinate role (Heim et al., 2021). The dominant soil types are Cryosols (IUSS Working Group WRB, 2015), which develop in silty, loess-like parent material (Figure S2). Organic layer thickness was generally low on all burnt and unburnt sites. The main causes for fires in the region are lightning strikes (Kornienko, 2018). However, the number of human-induced fires has recently increased due to the expansion of transport and settlement infrastructure in the course of oil and gas exploitation (Mollicone et al., 2006; Vilchek & Bykova, 1992; Yu et al., 2015).

2.2 | Sampling design

To examine the long-term impact of fire on biodiversity, we compared plant and bird communities in three large fire scars and adjacent unburnt control sites. All three fire scars were spatially close together (<10 km distance between scars) and, therefore, had rather similar environmental conditions. Fire scars were visually detected with annual Landsat images back to the year 1985 in Google Earth Timelapse (Gorelick et al., 2017) and with older Landsat images back to 1973 (U.S. Geological Survey, 2018). Areas that appeared pale (because of high lichen cover) on the images were considered as unburnt, while areas that switched from pale to dark were classified as fire scars. Those fire scars were characterized by an irregular shape, and their borders were often defined by meandering brooks. The oldest fire scar (3500 ha) was already visible on the first satellite image we used from 1973 (Landsat1) and therefore burnt at least 44 years ago. The next oldest scar (ca. 12,500 ha) burnt in 1990, and the youngest (542 ha) burnt in 2005.

The fieldwork took place in July 2017 (at the areas burnt before 1973 and in 2005) and July 2018 (at the area burnt in 1990). Therefore, the time since fire was 12, 28 and at least 44 years for the youngest, medium-age and oldest scar respectively. During fieldwork, the occurrence of fires was confirmed by signs of burnt trees and charcoal on the ground. We assumed that sampling in subsequent years was unlikely to bias the results, because environmental conditions of the tundra ecosystem are rather stable with low interannual variability (Dahl, 1975) and because climatic conditions in the two sampling years were similar (Kazakov, 2019).

2.2.1 | Sampling of vascular and non-vascular plants

To compare fire effects on vascular and non-vascular plants, we selected 10 sampling sites on each of the three fire scars along the fire border, which were located at least 300 m from each other. At each location, we placed one sampling plot onto the fire scar and one control plot onto unburnt tundra nearby. This resulted in 60 plots of 10 × 10 m (30 pairs). The two plots of each pair were situated as close as possible. Because minimum plot distance to the scar border was at least 50 m to avoid edge effects, the plots of one pair were at least 100 m apart. On each plot, we estimated the cover of all species (vascular plants, liverworts, mosses, lichens). We visually assessed the relative area of the plot covered by a plant species in cover percentages from different perspectives of the plot. Nomenclature follows The Plant List (2013) for vascular plants, Kristinsson et al. (2010) for lichens and Hodgetts et al. (2020) for bryophytes. When we refer only to 'plants' in the following text, we are referring to vascular and non-vascular plants.

On burnt areas of the youngest and medium-aged fire scars, the active layer was significantly deeper (mean values of change with 2.5% and 97.5% quantiles of the posterior distributions for the 12 year old fire scar: −33.02, −44.53, −20.66, and for the 28 year old fire scar: −32.20, −43.61, −20.58) and the soil temperature in 12 cm depth was significantly warmer compared to unburnt control areas (mean values of change with 2.5% and 97.5% quantiles of the posterior distributions for the 12 year old fire scar: 6.29, 4.61, 8.19, and for the 28 year old fire scar: 6.29, 4.48, 8.02), but after >44 years since fire, both the active layer depth and the soil temperature returned to levels of the unburnt area (mean values of change with 2.5% and 97.5% quantiles of the posterior distributions for active layer depth: −6.62, −5.18, 17.74 and soil temperature: 0.24, −1.52, 1.97) (Heim et al., 2021). Fire severity (delta Normalized Burn Ratio values of all burnt plots related to the fire scars burnt in 2005 and 1990) did not significantly differ between plots on the medium-aged scar and the youngest scar (Heim et al., 2021). For the oldest fire scar, no data regarding fire severity were available (Heim et al., 2021).

2.2.2 | Bird survey

To estimate bird species richness and model population densities, we conducted transect counts using a distance sampling approach (Buckland et al., 2015). We placed 16 transects (each with a length of 500 m) in each of the three fire scars and in the unburnt area (32 km survey effort and 64 transects in total). The transects in the unburnt area were placed centrally between the fire scars (minimum and maximum distance from control transects to fire scars in km: $\text{min}_{12\ \text{years}} = 5.71$, $\text{max}_{12\ \text{years}} = 11.90$, $\text{min}_{28\ \text{years}} = 1.00$, $\text{max}_{28\ \text{years}} = 5.66$, $\text{min}_{>44\ \text{years}} = 3.55$ and $\text{max}_{>44\ \text{years}} = 13.53$). Transects within one category were always parallel to each other, and all transects were at least 500 m apart. All transect counts were conducted from 12 to 20 July 2018 between 1 and 7 a.m. on days without rain or strong winds by the second author W. Heim.

We assigned each observation to one of five established distance classes (0–5 m, 5–10 m, 10–25 m, 25–50 m, 50–100 m, 100–200 m and 200–500 m) by using a laser range finder. Nomenclature follows BirdLife International (2020). The observed species were assigned to three groups based on the situation of their main breeding range from the literature (Billerman et al., 2020): tundra species, taiga species and species which occur both in tundra and taiga (Table S4).

2.3 | Statistical analysis

We used R, Version 4.0.3. (R Core Team, 2020) for all statistical analyses and fitted all models in a Bayesian framework using the function brm() from the package *brms* (Bürkner, 2017, 2018). For testing anticipated outcome 1 (alpha diversity follows the intermediate disturbance hypothesis over decades of post-fire vegetation succession), we fitted different linear models with different diversity measures (total species richness, Shannon index, evenness) as the dependent variables, and we used years after fire event (control, 12, 28, >44) as the independent categorical variable for plants and birds.

Because of the paired sampling design, we included pairs as a random intercept in all models for plants (Bates et al., 2015). In the models for species richness (count data) in plants and birds, we used Poisson distribution and log-link. This was also done for vascular plants, lichens and bryophytes separately. For model convergence we had to adapt delta to 0.99 in the model for lichens. We modelled Shannon index, for plants and birds separately, with a Gaussian distribution. Evenness in plants and birds was modelled with Gamma distribution and log-link. For model convergence we had to adapt delta to 0.99 in this model.

To obtain the posterior distribution, we used default priors of the *brms* package (Bürkner, 2017) and ran 4000 iterations (warmup = 2000) with four chains. The posterior distribution is a probability distribution that summarizes updated beliefs about the parameter after observing the data and is thus a result of the prior distribution and the likelihood function (Korner-Nievergelt et al., 2015). The posterior distribution is a probability distribution that summarizes updated beliefs about the parameter after observing the data; thus, it is a combination of the prior distribution and the likelihood function (Korner-Nievergelt et al., 2015). In Section 3, we present mean values and the 95% credible interval (CrI) of the simulated posterior distribution. The 95% CrI is the range in which the true value is expected with a probability of 0.95, and which is limited by the 2.5% and the 97.5% quantile of the posterior distribution. Not overlapping CrIs imply a significant difference at alpha = 0.05 between groups. If the estimated mean value for the intermediate fire scar would be higher than the mean value for the control area, and the CrIs of both are not overlapping, the intermediate fire scar would have a significantly higher estimated value than the control. If the mean of the youngest fire scar would be higher than the mean value for the control area, but the CrIs of both are overlapping, the youngest fire scar would not have a significantly higher estimated value than the control.

To test anticipated outcome 2 (alpha diversity in vascular and non-vascular plants decreases with increasing shrub cover), we modelled the relationship of deciduous shrub cover and plant diversity using Poisson distribution and log-link including total, vascular, lichen and bryophyte species richness as the dependent variables and deciduous shrub cover and its quadratic term as the independent variables. We excluded one value with very high shrub cover (40% higher than next highest value) from this analysis, as this shrub cover value was likely a data entry error. Plot pairs were included as a random factor.

Shannon index was included as a dependent variable in a model with Gaussian distribution, with deciduous shrub cover and its quadratic term as independent variables. Evenness was modelled in the same way with a Gamma distribution and a log-link. We calculated the posterior probabilities as described for anticipated outcome 1. Impact of deciduous shrub cover and years after fire with interaction were not included in one model because of collinearity (variance inflation factor >5).

For anticipated outcome 3 (proportion of southern [taiga] bird species is highest on fire scars with high shrub cover) we fitted a model with logit-link and binomial error distribution. We included the proportion of taiga bird species per transect as the dependent variable using the total number of detected species on an individual transect (tundra birds, taiga birds and species occurring in both habitats) as baseline (total number of species on transect/taiga species). Years after fire was included as categorical independent variable. Again, the posterior probabilities were calculated as described for anticipated outcome 1.

For anticipated outcome 4 (multiple fire scars of different ages temporarily increase biodiversity at the landscape scale), we fitted Euler diagrams for shared species, generated with the help of the eulerr package (Larsson, 2020).

For anticipated outcome 5 (even after >44 years, plant and bird species composition still differ from pre-fire conditions), we performed an indicator species analysis for plants and birds with the package *indicspecies* (De Caceres & Legendre, 2009); this allowed us to identify and compare species which are associated with control and burnt areas. We only allowed single group affiliations.

We furthermore performed ordinations for plants and birds with self-organizing maps (SOMs) using the package *kohonen* (Wehrens & Buydens, 2007). Artificial neural networks (ANNs) are increasingly used in ecology as they are useful for modelling complex biological and environmental data (Shanmuganathan et al., 2006). The Kohonen SOM is an ANN that learns to represent multidimensional input data in a low-dimensional space through an unsupervised learning algorithm (Kohonen, 2012). The SOM consists of two layers of artificial neurons, the input layer, which is fed by external data (here species tables of plants and birds), and the output layer, which is usually a two-dimensional map out of hexagons. Every neuron in the output map and every input neuron is connected, and each connection has a weight (Chon, 2011). The SOM algorithm aims to display the sample units (in our case plots and transects) of the input data by performing several steps: (1) The distance between one random sample unit and

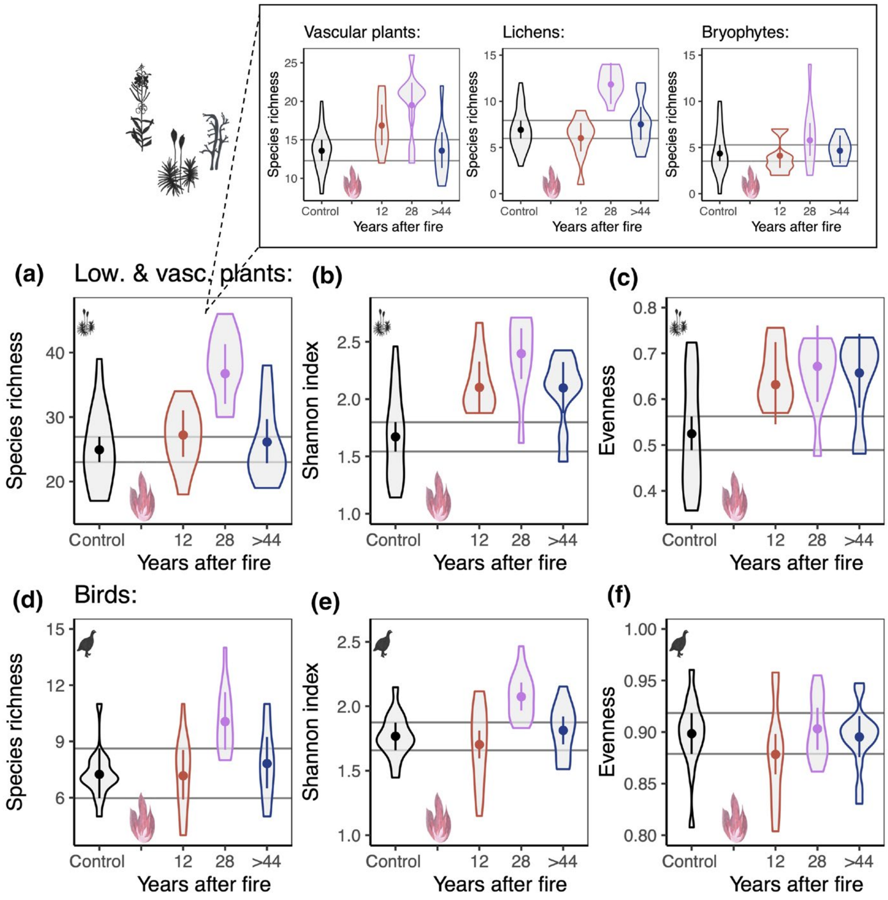

FIGURE 1 Species richness (a, d), Shannon index (b, e), and evenness (c, f) of vascular plants, lichens, bryophytes and birds on control and burnt areas (12, 28 and >44 years after fire). Violin plots show the continuous distribution of raw data, black dots are predicted mean values and vertical lines are 95% credible intervals (CrIs). Grey horizontal lines show the borders of the control group's CrI. Low. & vasc. Plants: Non-vascular and vascular plants

each hexagon is calculated by the learning algorithm, which looks for clusters in the input data (in our case based on species composition). (2) The hexagon with the smallest distance to the sample unit is chosen as a winner. (3) Weights are updated with the new information. During the training process, these steps are repeated with a random input sample for each training run (Giraudel & Lek, 2001).

SOMs are not widely known and used by ecologists, but this method has clear advantages for community ecology (Giraudel & Lek, 2001). SOMs allow for displaying non-linear species abundance patterns, which is difficult with traditional linear ordination methods like principal component analysis (Wehrens & Buydens, 2007). Another method that is a commonly used to avoid the problem of non-linear relationships is non-metric multidimensional scaling (NMDS), but the results of NMDS depend on the number of axes included (Giraudel & Lek, 2001)and NMDS often ends up with a multi-dimensional space, which is difficult to display and understand (Wehrens & Buydens, 2007).

Next, we analysed the impact of fire on the six most abundant plant and bird species. For the plant species, we fitted a linear mixed-effects model for each species with cover as the dependent variable and years after fire event (control, 12, 28, >44) as categorical independent variable. We used a zero-inflated beta distribution and plot pairs were included as a random factor. We calculated the posterior probabilities as described for anticipated outcome 1. For model convergence we had to adapt delta to 0.99 in the model for *Cladonia stellaris*, *Vaccinium uliginosum* and *Carex globularis*.

For bird densities, we fitted a hierarchical distance sampling model for each species independently, to correct for factors that affect detection probability (Kéry & Royle, 2016). We used the function *gdistsamp* of the package *unmarked* (Allaire et al., 2019), which can be used for a negative-binomial abundance distribution. We expected time after sunrise to impact detection probability, as birds are most active during sunrise or shortly after (Robbins, 1981) and, thus, we included this variable (and its quadratic term) in our models in the detection function part. The variable sunrise was not important in all models and was therefore not included in all final models. We included years after fire in the abundance part of the model and the availability part was always ~1. In all final models, we used the half-normal detection function, as the models did not converge using hazard rate or uniform detection function, and negative exponential detection function performed poorly (high AIC).

3 | RESULTS

3.1 | Fire influence on alpha diversity and shared species

Across all sites, we recorded a total of 51 vascular plant species, 27 bryophyte and 33 lichen species and 28 bird species (Table S3, Table S4). Fire significantly influenced diversity patterns in plants and birds (Figure 1, Table S5). We found that species richness was highest at the intermediate-age (28 years old) fire scar in plants and birds. Also, the Shannon index was highest at the intermediate-age fire scar in plants and birds. As a rule, at fire scars (compared to unburnt control plots), the Shannon index for vascular and non-vascular plants was higher and the community was more even. Species richness and Shannon index in birds reached control levels after 12 and >44 years but was higher on the intermediate fire scar. Shannon index for vascular and non-vascular plants did not differ between fire scars. Evenness in plants and birds did not differ between the fire scars. While the older fire scars showed a higher evenness than the control in plants, fire did not influence bird community evenness.

3.2 | Impact of shrub cover on species richness of vascular and non-vascular plants

Deciduous shrub cover influenced species richness of all plants in a hump-shaped manner with maximum species richness occurring when the percentage of shrub cover was neither very high nor very low (Figure 2, Table S6). This relationship was mainly driven by vascular plants and lichens, as we found no evidence that shrub cover influenced bryophytes. Shannon index and evenness of plants were lowest at the minimum shrub cover value, and they reached maximum values at higher levels of shrub cover.

3.3 | Proportion of southern (taiga) bird species

The proportion of southern (taiga) bird species was highest in the oldest fire scar while the proportion in the younger fire scars did not differ compared to the control (Figure 3, Table S7).

3.4 | Shared species

We found 35 plant species and 12 bird species shared by control and burnt areas (Figure 4). While 14 plant species were only found in control and not in burnt plots, fire disturbance led to 18 additional plant species only found in burnt areas. Only one bird species was exclusively found in unburnt areas, while eight species were confined to burnt areas.

3.5 | Fire effects on plant and bird community composition

3.5.1 | Indicator species

The indicator species analysis for vascular plants, lichens and bryophytes revealed that the unburnt control plots are characterized by two dominant lichen species, while different bryophyte and vascular plant species are characteristic of burnt sites (Table 1). *Epilobium angustifolium* was found to be an indicator species for the youngest fire scar, while the intermediate-age fire scar is characterized by many less abundant vascular plants, moss and lichen species. *Betula nana* is one of the indicator species found for the oldest fire scar. The bird indicator species for the control plots is *Motacilla flava*, a species preferring

TABLE 1 Plant indicator species for unburnt control and burnt areas with indicator and *p*-value

Years after fire	Species	Indicator value	*p*-value
Control	*Cladonia stellaris*	0.82	.001
	Cladonia rangiferina	0.78	.001
	Flavocetraria cucullata	0.72	.019
12	*Polytrichum commune*	0.85	.002
	Pedicularis labradorica	0.66	.008
	Epilobium angustifolium	0.64	.004
	Vaccinium uliginosum	0.61	.048
	Stellaria longipes	0.58	.015
	Poa alpigena	0.57	.027
	Cladonia botrytis	0.51	.029
28	*Cladonia cyanipes*	0.95	.001
	Cladonia macrophylla	0.93	.001
	Polytrichum juniperinum	0.89	.012
	Cladonia sulphurina	0.84	.002
	Stereocaulon paschale	0.83	.001
	Salix glauca	0.82	.001
	Baeomyces carneus	0.79	.007
	Aulacomnium turgidum	0.77	.002
	Arctagrostis latifolia	0.74	.009
	Lycopodium annotinum	0.72	.001
	Cladonia borealis	0.70	.001
	Lycopodium lagopus	0.69	.004
	Ledum palustre	0.65	.031
	Diphasiastrum complanatum	0.63	.001
	Cladonia uncialis	0.63	.004
	Cladonia coccifera	0.63	.039
	Salix viminalis	0.62	.003
	Festuca ovina	0.61	.002
	Dicranum flexicaule	0.59	.035
	Equisetum pratense	0.55	.011
	Cladonia chlorophaea s.l.	0.54	.025
	Tofieldia coccinea	0.54	.015
	Pohlia nutans	0.50	.019
	Flavocetraria nivalis	0.48	.037
>44	*Pleurozium schreberi*	0.81	.001
	Salix myrtilloides	0.69	.005
	Betula nana	0.62	.004

Note: We included only species with an occurrence ≥3

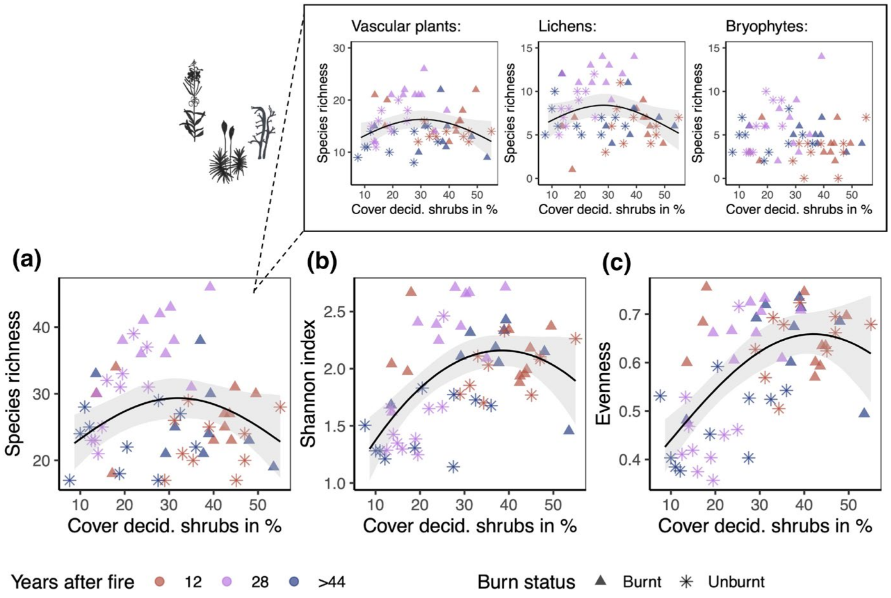

FIGURE 2 Species richness (a), Shannon index (b), and evenness (c) of vascular plants, lichens and bryophytes on control and burnt areas (12, 28 and >44 years after fire). Coloured symbols are raw data. Black lines are predicted mean values, with 95% credible intervals (CrIs) in grey. Decid. shrubs: deciduous shrubs

open habitats. In contrast to that, the oldest fire scar is characterized by shrub-dwelling species, including typical taiga species such as *Phylloscopus inornatus* (Table 2). As for plants, the highest number of indicator species in birds was found at the intermediate-age fire scar.

3.5.2 | Species composition

The species composition of plants and birds on the unburnt control sites was relatively similar, indicated by the clustering of control plots and transects in the centre of the SOM output maps (Figure 5). In contrast, many plots and transects of the burnt sites were located on the outer margins on dark-coloured neurons of the maps, revealing that fire led to a more distinct species composition.

The output map for vascular and non-vascular plants illustrated that the fire scars differed in species composition depending on the age of the scar, as the plots for each burnt area clustered in different parts of the output map. The output map for birds showed that the intermediate-age fire scar stands out regarding species composition, evident through the bottom-left cluster. In contrast, the youngest and oldest fire scars had similar bird species compositions, as indicated by the overlapping transects of these fire scars.

For the output maps of plants and birds, the locations of the fire scar sites were reflected by the probability of occurrence of the indicator species. *Polytrichum commune*, for example, which is a bryophyte species and indicator species for the youngest fire scar, showed the highest probability of occurrence in output neurons where plots of the youngest fire scar were located.

3.5.3 | Fire impact on most abundant species

We found that cover of the most abundant vascular and non-vascular plant species was influenced by fire trajectories (Figure 6, Table S8). Cover of the two lichen species *Cladonia stellaris* and *C. rangiferina* was reduced by fire and did not reach control levels even after >44 years, while cover of the shrub species *Betula nana* and *Ledum palustre* was higher on the older fire scars in comparison to the unburnt plots.

Regarding the densities of the most abundant bird species, we found no significant differences between burnt and unburnt areas, but a tendency towards increased densities of shrub-dwelling species such as *Phylloscopus* warblers in the oldest fire scar.

4 | DISCUSSION

4.1 | Fire influences alpha diversity in vascular plants, lichens, bryophytes and birds

Tundra fires can have strong and strikingly long-lasting effects on diversity patterns of plants and birds. Our study indicates a significant increase in diversity of plant and bird species at the intermediate-age fire scar, which confirms our first anticipated outcome (alpha diversity of plants and birds is highest at an intermediate timescale after fire). An increase in species richness with time since fire on burnt areas reflects the dispersal of species and was also described for Afroalpine heathlands (Hylander et al., 2021) and subalpine Rocky Mountain vegetation (Coop et al., 2010). The hump-shaped pattern in our study might be explained by the intermediate disturbance hypothesis (Connell, 1978), as early and late successional species build a common species pool at an intermediate recovery state. Later successional states, like undisturbed tundra areas, are characterized by the dominance of single species (e.g. the lichen *Cladonia stellaris*) and show a reduced species diversity (Ahti & Oksanen, 1990). A peak of lichen species richness 30–40 years after fire was earlier described for the Alaskan tundra (Holt et al., 2008). However, those findings stay in contrast to other investigations in Australian alpine heathlands that did not find a support of the intermediate disturbance hypothesis, by investigating fire severity instead of the successional timescale (Camac et al., 2013).

We show an increase in plant species richness when deciduous shrub cover is neither very high nor very low. As we anticipated that alpha diversity in vascular and non-vascular plants decreases with increasing shrub cover, our result only partly followed our second anticipated outcome. The low species richness at early successional states might be less driven by shrub cover but, instead, more driven by the recent disturbance or by the dominance of other plant types (e.g. cover of graminoids or dwarf shrubs). Disturbance effects may last for a relatively long time, as the establishment and recovery of tundra species, especially lichens, takes several decades (Jandt et al., 2008). In the late successional states, high shrub cover leads to reduced light availability and, thus, to an overall decrease of species richness (Myers-Smith et al., 2011; Pajunen et al., 2011).

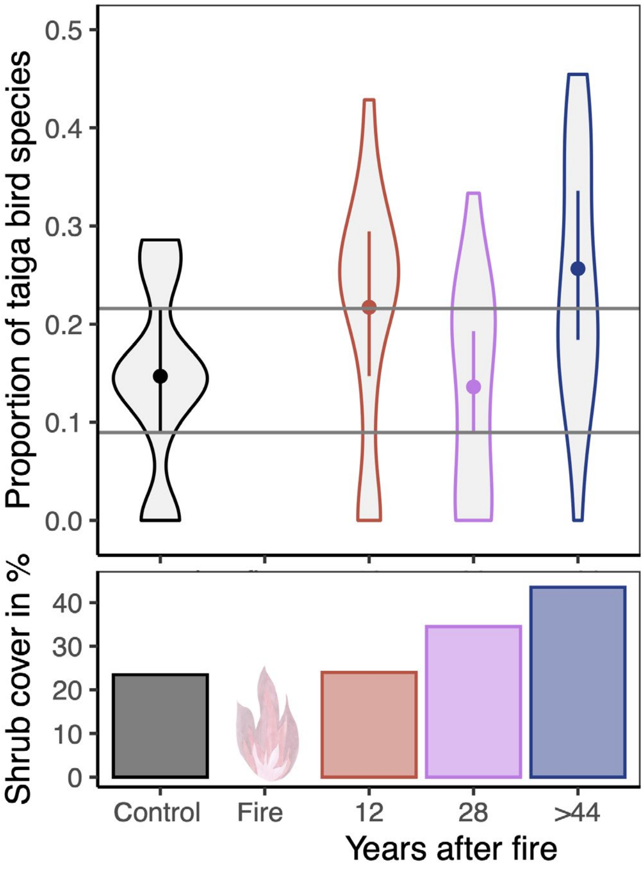

FIGURE 3 Proportion of southern (taiga) bird species on control and burnt areas (12, 28 and >44 years after fire). Violin plots show the continuous distribution of raw data, dots are predicted mean values and vertical lines are 95% credible intervals (CrIs). Grey horizontal lines show the borders of the control group's CrI. Bar plots show mean shrub cover for all four areas

We found that the proportion of southern (taiga) bird species is highest in the oldest fire scar, mirroring the increase in shrub cover (confirming anticipated outcome 3: the proportion of southern [taiga] bird species is highest on fire scars with high shrub cover). This relationship demonstrates that climate change-related shrub expansion in tundra ecosystems (Davis et al., 2021; Kitagawa et al., 2020; Myers-Smith et al., 2011) could indeed lead to range expansion and increased abundance of southern bird species in tundra ecosystems (Elmhagen et al., 2015; Ktitorov et al., 2021;

TABLE 2 Bird indicator species for unburnt control and burnt areas with indicator and *p*-value

Years after fire	Species	Indicator value	*p*-value
Control	*Motacilla flava*	0.53	.040
12	*Gallinago stenura*	0.45	.045
28	*Pluvialis apricaria*	0.89	.001
	Lagopus lagopus	0.61	.001
	Numenius phaeopus	0.59	.004
	Anthus cervinus	0.58	.002
	Luscinia svecica	0.57	.042
	Emberiza pallasi	0.51	.025
	Turdus eunomus	0.50	.014
>44	*Phylloscopus inornatus*	0.58	.021
	Emberiza pusilla	0.57	.033
	Phylloscopus trochilus	0.56	.006

Note: We included only species with an occurrence ≥3.

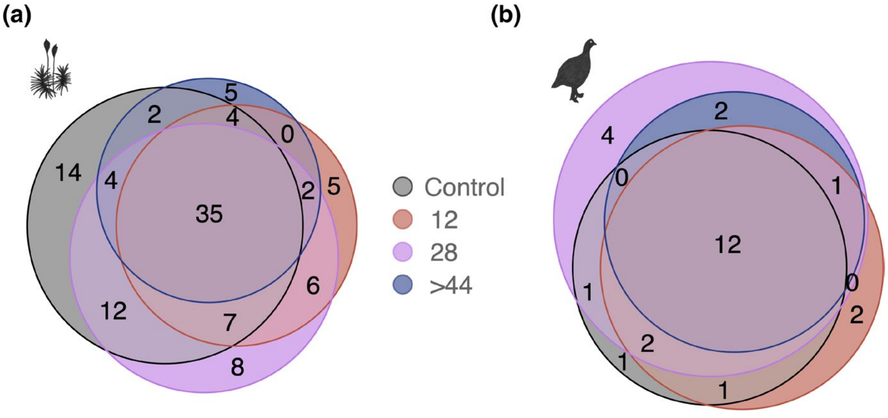

FIGURE 4 Shared species for (a) plants (vascular and non-vascular) and (b) birds on unburnt control and burnt areas (12, 28 and >44 years after fire)

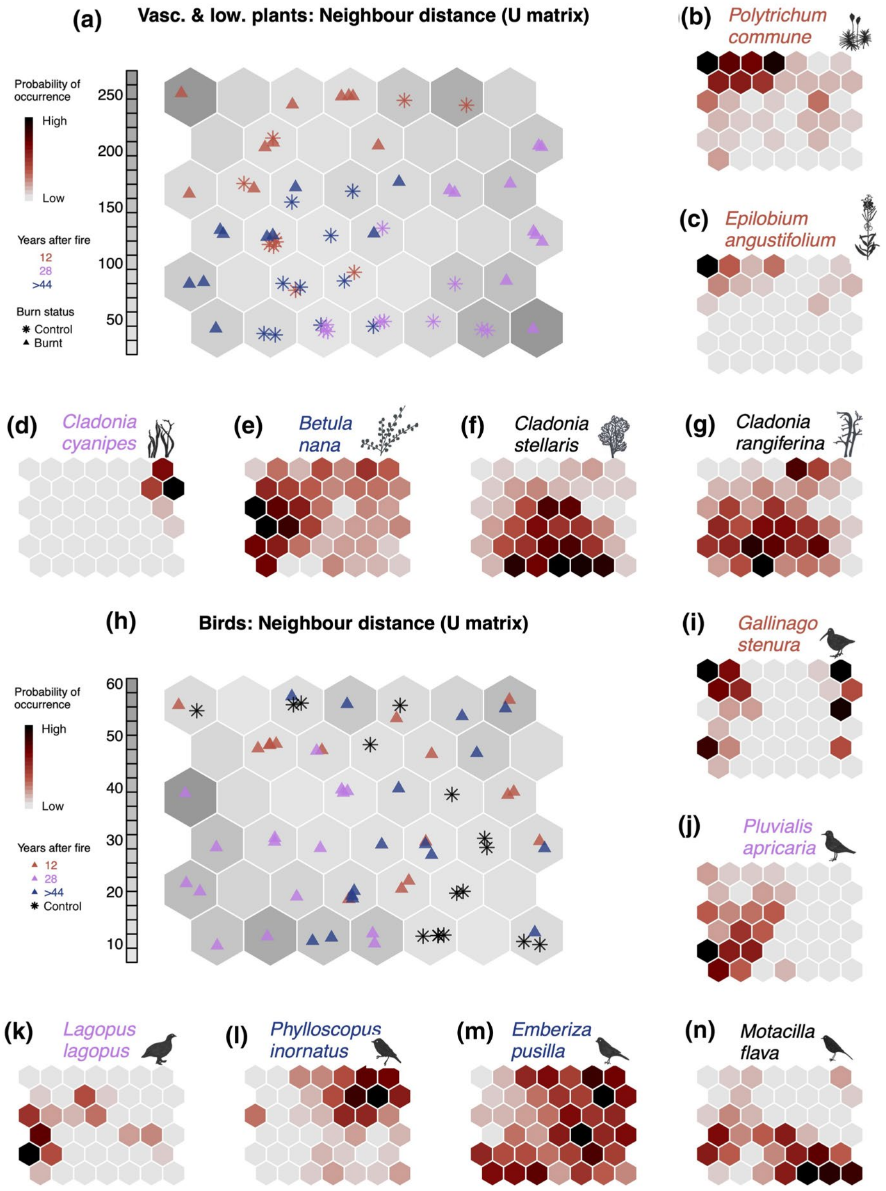

FIGURE 5 Self-organizing map (SOM) output neurons for plants and birds, displaying distance between neurons (U-matrix) in grey colours and assigned plants plots and bird transects of control and burnt areas (a and h). A long distance from neighbour neurons is displayed by dark grey, while a close distance to neighbour neurons is displayed by light grey. Species-related maps (b–g and i–n) show the probability of occurrence of six selected plants and bird indicator species related to the output neurons of the main map. For example, *Polytrichum commune* (b) is an indicator species for the youngest fire scar and has a high probability of occurrence in those output neurons in which plots of the youngest fire scar are located in the main map

Smith et al., 2020). However, warming-related shifts towards more boreal species in the Arctic fauna have also been observed in seabird communities that are not related to shrub cover (Descamps & Strøm, 2021).

Furthermore, we were able to show that the fire scars of different ages enhanced biodiversity at the landscape scale through species that were only found on burnt areas. This is in line with the pyrodiversity–biodiversity hypothesis, which claims that landscapes with fire scars of different ages exhibit higher spatio-temporal habitat heterogeneity (He et al., 2019). However, the enhanced species diversity is mainly related to species that are disturbance indicators (e.g. *Epilobium angustifolium*) and/or southern species that are not typical of subarctic tundra habitats.

Depending on the region with its fire history and characteristics, burning can have an overall positive effect on the diversity of alpine and tundra ecosystems as shown for examples in Afroalpine heathlands (Hemp, 2006; Johansson et al., 2018). However, this cannot be generalized as studies from North American tussock tundra showed lower Shannon diversity in burnt areas in comparison to unburnt control, 10 and 14 years after fires (Jandt & Meyers, 2000; Narita et al., 2015). Such divergent findings may be due to differences in fire severity and frequency that have been shown to influence vegetation succession (Hewitt et al., 2016; Hollingsworth et al., 2021).

4.2 | Post-fire species composition of vascular and non-vascular plants

We found no recovery of the plant species composition to the pre-fire state, even after >44 years of post-fire succession. This adds to the growing number of studies documenting no recovery of plant species composition in tundra after fire (Ahti & Oksanen, 1990; Bret-Harte et al., 2013; Narita et al., 2015; Tsuyuzaki et al., 2018).

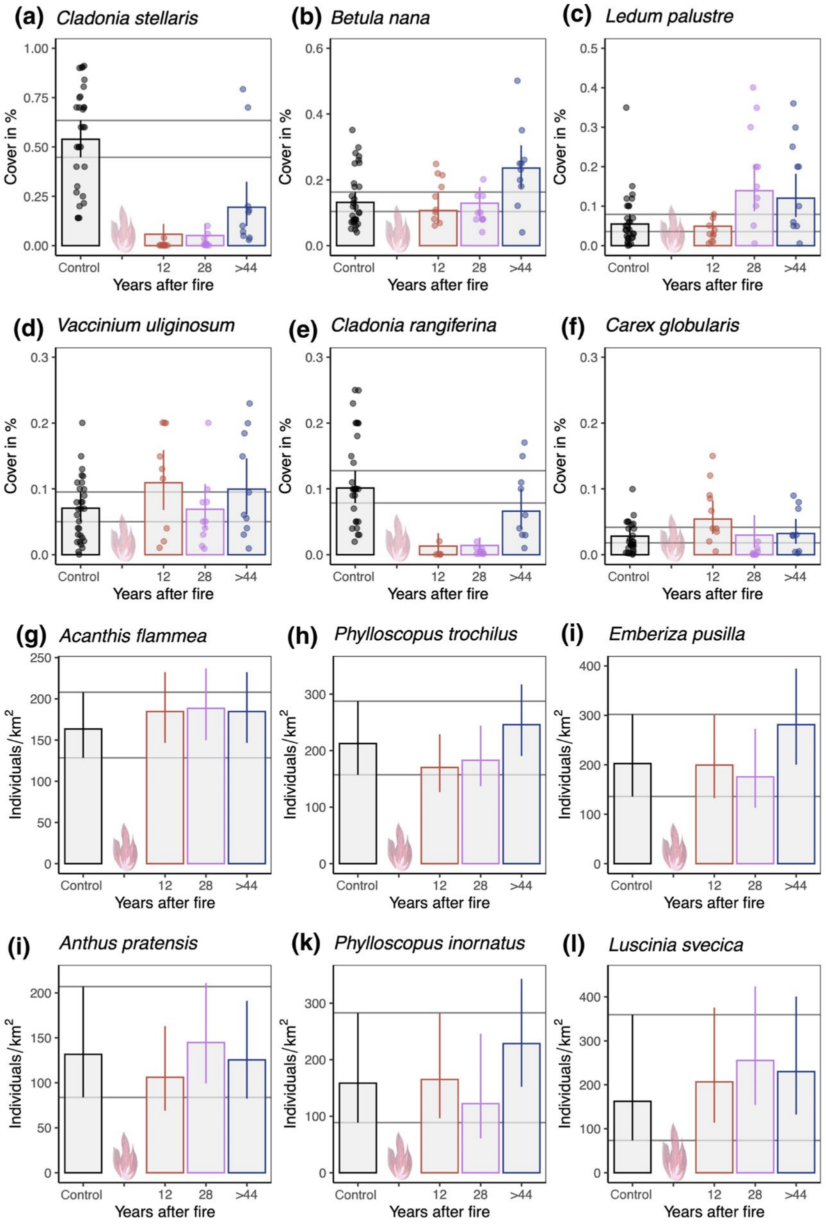

FIGURE 6 Cover of the six most common plants species (a–f; ordered by decreasing total cover) on control and burnt areas (12, 28 and >44 years after fire). Coloured dots are raw data. Bar plots show predicted mean values and coloured lines show 95% credible intervals (CrIs). Grey lines show the borders of the CrI of the control group. Densities of the six most common bird species (g–l; ordered by decreasing abundance) on control and burnt areas (12, 28 and >44 years after fire) from a hierarchical distance sampling model. Bar plots show predicted mean values and coloured lines show 95% confidence intervals (CIs). Grey lines show the borders of the control group's CI. Non-overlapping CIs imply a significant ($p < .05$) difference between groups

The indicator species analysis for plants revealed that undisturbed tundra in our study area is characterized by *Cladonia* lichens, especially reindeer lichens of the *Cladonia* subgenus *Cladina*. The two most abundant species, *Cladonia stellaris* and *C. rangiferina*, did not reach pre-fire cover levels after >44 years. This is consistent with earlier studies describing slow recovery of tundra lichens after fire disturbance (e.g. Jandt et al., 2008). The lack of mat-forming lichens after fire is likely a key driver for the observed changes in species communities due to drastic changes in microclimate and ecological processes (Mallen-Cooper et al., 2021; Roos et al., 2021).

At early successional stages after fire, *Epilobium angustifolium* has been found as an indicator species; this plant is a widespread ruderal generalist species commonly benefiting from disturbance, including fire disturbance in tundra (Tsuyuzaki et al., 2018). In accordance with our study, *Polytrichum* species are known to be early successional species in boreal forests (Schimmel & Granstrom, 1996) and heaths (Ruokolainen & Salo, 2009).

The intermediate-age fire scar is distinct due to its many bryophyte and lichen indicator species, which had the chance to establish during the 28 years after the fire without being outcompeted by more dominant species. Moreover, the intermediate-age fire scar is also characterized by a large collection of vascular plant indicator species. The high species richness found for this fire scar, linked to an intermediate timespan after disturbance, corroborates the intermediate disturbance hypothesis for the subarctic tundra.

The oldest fire scar in our study is characterized by the indicator species *Betula nana*, a species known to dominate shrub expansion in tundra regions (e.g. Deslippe & Simard, 2011), which underpins the importance of *Betula nana* in shaping long-term post-fire succession of the tundra ecosystem (e.g. Bret-Harte et al., 2001; Mallen-Cooper et al., 2021). This is in line with findings from other regions, such as the Australian Alps, where similar processes of fire promoting shrub encroachment were shown (Camac et al., 2017).

One indicator species for the oldest fire scar was *Pleurozium schreberi*, which has been described in North American studies as an important species for a late recovery stage (51 years and onwards) (Foster, 1985; Scotter, 1964).

In our study, we demonstrated that the cover of *Cladonia stellaris* and *Cladonia rangiferina* on fire scars strongly increased with time since fire, which is in line with Ahti (1959) and Scotter (1964), who described a full recovery of lichen cover at 80 or 120 years after fire in boreal North America.

4.3 | Post-fire species composition of birds

Bird species composition differed between control and burnt areas, even after >44 years (Figure 4). Nevertheless, this pattern was not as clear as in plant species composition. The species composition of birds at the intermediate-age fire scar was distinct, while the youngest and oldest fire scar showed similar species compositions. Considering that arctic bird communities can re-establish on burnt areas within a relatively short time period (Pérez et al., 2018), the differences in species composition observed decades after fire are likely driven by post-fire changes in vegetation structure. Vegetation plays a significant role in tundra food webs, as it directly influences herbivores and, therefore, arthropod abundance, thereby strongly impacting their avian predators (Schmidt et al., 2017). The distinct bird species composition at the intermediate-age fire scar may be related to the high species diversity found for plants, providing a diverse food supply and vegetation structure. Remarkably, some larger non-passerine species such as *Numenius phaeopus*, *Pluvialis apricaria* and *Lagopus lagopus* showed a clear preference for this successional stage. The latter two species' positive associations with shrub cover have also been found in other studies (reviewed in Wheeler et al., 2018).

Our indicator species analysis clearly reflects the structural changes of the tundra vegetation after fire (i.e. from an open and lichen-dominated unburnt subarctic tundra to shrub-dominated successional stages). While *Motacilla flava*, a species that lives in open habitats, most commonly in lowland shrub tundra in the region (Sokolov et al., 2012), was found as an indicator species for the unburnt control, whereas indicator species for the oldest fire scar mostly consist of shrub-dwelling species with a more southern distribution, such as *Phylloscopus* leaf warblers and *Emberiza pusilla* (Sokolov et al., 2012). Shrub-dwelling songbird species increasingly join Arctic bird communities (Ktitorov et al., 2021). The indicator species for the youngest fire scar, *Gallinago stenura*, is known to occur in recently disturbed areas, for example, after forest clear cuts (Golovina, 1998). Also, particularly characteristic for the intermediate-age fire scar was wading birds preferring open, short-growing vegetation structures such as *Pluvialis apricaria* and *Numenius phaeopus*. Similar to plants, most indicator species were found for the intermediate-age fire scar, illustrating the significant increase in species richness.

We did not detect significant post-fire trends in the densities of the six most abundant bird species in our study, most likely due to limited sample sizes. However, the abundance of some species, such as *Phylloscopus inornatus*, might be connected to fire, with the highest densities observed in the oldest fire scar. This species is known to occur in burnt areas and has recently expanded its north-western range border (Keller et al., 2020), which could be linked to increased habitat availability as a consequence of climate change. Based on these findings, we argue that fire-induced changes in vegetation structure could accelerate climate-driven alterations in tundra bird communities.

5 | CONCLUSION

Fire disturbance is an important driver of changes in long-term diversity and species composition in the subarctic tundra ecosystem of Western Siberia. We found that fire (at least temporarily) increased the biodiversity at the landscape level through fire scars of different ages. Although tundra fires may temporarily increase biodiversity, they will not reduce the actual threats to the biodiversity of the tundra; in fact, tundra fires may rather increase these threats in the long term.

Notably, fire disturbance may play an important role in predicting how northern ecosystems' biodiversity will change with future global climate changes. Our results imply that species composition in plants and birds does not recover to pre-fire states even after >44 years. On the contrary, our results show that fire reinforces climate-driven spread of encroacher species like *Betula nana*, at later successional stages. In turn, increased shrub abundance seems to impact species diversity relationships in lichens, vascular plants and birds. These long-term changes in community composition towards more woody biomass may promote the probability of future fire events (Higuera et al., 2008).

With the aim of understanding the impact of fire on the tundra ecosystem within the feedback loop of climate change and increasing fire events, this study fills an important knowledge gap. However, we could not determine whether the long-lasting changes after a fire simply require more than half a century to recover or whether tundra fires create irreversible shifts in terms of species composition.

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DATA AVAILABILITY STATEMENT

All data are openly available in 'Zenodo' at https://doi.org/10.5281/zenodo.5568292.

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