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Anthropogenic fire patterns affect niche breadth and niche overlap in sympatric songbird species

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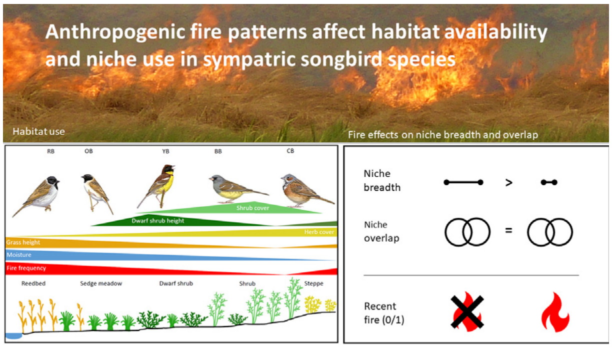
HIGHLIGHTS

- anthropogenic fires are increasing, but fire effects on niche separation are poorly understood
- we investigated occurrence, niche breadth and niche overlap in songbird species on recently burned and unburned patches
- recent anthropogenic fire did not affect occurrence in 4 out of 5 species, but fire frequency determined niche separation in 3 out of 5 species
- niche breadth was lower in recently burned patches, but niche overlap did not increase after recent fire despite decrease in habitat diversity
- anthropogenic fire alters niche breadth & community structure and should be considered when analyzing niches or species´ distribution

GRAPHICAL ABSTRACT



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ABSTRACT

The severity of wildfires increases globally, and return intervals decrease. Fires can benefit biodiversity, as post-burn early successional stages provide diverse habitats and niches for many species. How fire disturbance affects niche use and niche overlap of species is poorly understood so far. We studied the effect of anthropogenic fire on breeding habitat use, niche breadth and niche overlap of five sympatric bunting species breeding in wetlands of the Amur River floodplain (Russian Far East). Fire frequency, measured as the time an area burnt in the period 2000 to 2017, was mapped from Landsat imagery and related to the presence or absence of the species. Niche breadth and niche overlap were calculated separately for occurrences in burned (within the study year) and unburned patches. Fire frequency characterized differences in niche use among the species, but the probability of presence was not affected by recent fire in four of five species. Niche breadth was significantly lower in recently burned patches, but we found no increase in niche overlap between species after fire. Instead, the studied species seemed to occupy similar patches before and after fire, possibly because of a high site fidelity. Our results clearly show that fire frequency is a major determinant for the niche separation in the five studied species, while recent fire does not affect niche overlap.

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1. Introduction

With climate change, frequency and severity of wildfires increases globally (Williams, 2001; Brown et al., 2004; Moriondo et al., 2006; Flannigan et al., 2009; Dupuy et al., 2020; Kelly et al., 2020). Through the combustion of biomass, fires are known to significantly alter habitats and nutrient cycles (Hulbert, 1988; Flores et al., 2011; Stavi, 2019; Hrelja et al., 2020). Vegetation succession after fire can lead to a rapid turnover in species communities and can, therefore, benefit biodiversity (Fox, 1982; Potts et al., 2003). Furthermore, fire-induced population fragmentation may foster speciation processes (Cowling, 1987). In some fire-prone systems, functionally similar species may replace each other during succession, leading to functional stability (Moretti et al., 2009). Other reports have indicated an increase in functional diversity already shortly after fire (Arnan et al., 2013; Sitters et al., 2016).

Many studies have investigated biodiversity responses to fire, but less is known about how fire affects species' environmental niche use (sensu Grinnel, 1917). Niche segregation is generally assumed among congeneric, sympatric species (Begon et al., 2006). A study with *Sylvia* warblers found very weak phylogenetic effects on their ecological niches (Böhning-Gaese et al., 2003), implying that closely related bird species quickly adapt to changed environmental conditions. While most applications of ecological niche theory focus on climatic and edaphic variables to predict species occurrence, top-down drivers such as fire are now increasingly considered (e.g. Reside et al., 2012; Staver et al., 2012; Crimmins et al., 2014; Bradley et al., 2018; Rayfield et al., 2021). Fires can be the main determinant of ecosystem structure in fire-prone biomes (Bond et al., 2005), and neglecting fire as a driver of niche partitioning will result in unrealistic predictions of species' occurrences.

While in some cases fire may mediate niche separation between animal species through increased structural diversity of vegetation (Mowat et al., 2015), in other cases fire may instead reduce the vegetation structure, thus leading to increased niche overlap between species (Spowart and Hobbs, 1985). Structural vegetation heterogeneity is often lowest after recent fire, and highest at intermediately burned sites (Levick et al., 2009; Beal-Neves et al., 2020). Further, the effects of fire on species' presence or abundance has also been linked to species-specific niche breadth: In Korean butterfly communities, specialist species with narrow niches decreased occurrence after fire (Kwon et al., 2013), while in Mediterranean bird and reptile communities, specialist species increased with fire frequency (Moreira et al., 2001; Santos and Cheylan, 2013). Generally, specialist species with a narrow niche are expected to decline after disturbances, while generalist species often thrive (Futuyma and Moreno, 1988; McKinney and Lockwood, 1999). For some species, their niche (i.e. the preferred condition) is destroyed by fire, and they will have to recolonise burnt areas from unburnt refugia (Aylward et al., 2015).

However, our knowledge on the potential of fire to increase competition between species is biased towards ecosystems where species' have adapted to natural wildfires. Data on the potential effects of increasing anthropogenic fires on niche breadth and niche overlap of co-occurring species are lacking. Understanding such changes in species' niches is key for predicting species' distributions in the light of global change (Pearman et al., 2008; Warren et al., 2008; Broennimann et al., 2012; Saupe et al., 2019).

Here, we ask whether anthropogenic fire causes changes in habitat use, niche breadth and niche overlap among a group of five sympatric bunting species (Emberizidae) breeding in wetlands along the Amur River in the Russian Far East: the reed bunting *Emberiza schoeniclus* (RB), the yellow-breasted bunting *E. aureola* (YB), the chestnut-eared bunting *E. fucata* (CB), the black-faced bunting *E. spodocephala* (BB) and the ochre-rumped bunting *E. yessoensis* (OB). These species are known to exhibit subtle differences in habitat preferences in grasslands not affected by fire (Nakamura et al., 1968). In our study area, frequent anthropogenic fires are known to reduce shrub and litter cover (Heim et al., 2019, 2021), which is likely limiting key habitat elements for our study species. To address the knowledge gap regarding anthropogenic fires effects on niche breath and niche overlap in co-occurring species, we test the following predictions:

- niches of the studied species are well separated in unburned patches.
- recent fire homogenizes vegetation structure, thereby leading to increased niche overlap on burned patches.
- species with a wide niche are unaffected by or favoured by fire, whereas species with a narrow niche have a lower probability of occurrence in burned patches.

2. Materials and methods

2.1. Study site

Field work was conducted as part of the Amur Bird Project (Heim and Smirenski, 2013, 2017) from May to July 2017 at the Muraviovka Park for Sustainable Land Use (49°55 N, 127°40 E), a nature reserve in the Amur region of the Russian Far East. The study area (8169 ha) is part of the Amur River floodplain and is characterized by extensive sedge meadows, willow shrub, elevated steppe islands and small woodland patches (see land cover map based on Richter et al., 2020 in Supplement 1). The climate is temperate continental, with a high temperature amplitude between winter (January mean −32 °C) and summer (August mean 23 °C), dry winters and springs and maximum precipitation in summer (Simonov and Dahmer, 2008). Anthropogenic fires occur very frequently at a mean fire return interval of 2.53 years in wetlands (Heim et al., 2019; Smirenski et al., 2018). Fires originate from post-harvest straw burning on arable fields, from open fireplaces or garbage dumps, or are set intentionally by poachers (Smirenski et al., 2018; Heim et al., 2019). Almost the entire study area is affected by anthropogenic fire, with most of the wetlands having burned more than five times during the years 2000–2017 and only few agricultural fields not having burned once in the same time frame. “Natural” wildfires in the wetland areas have not been observed in the past 20 years, as wildfires are usually limited to forest areas in the Russian Far East (Yu et al., 2017; Hayasaka et al., 2020). Fires in our study area usually cause a complete combustion of aboveground parts in herbaceous plants, but burned stems of trees and bushes with a potential to resprout often remain after fire.

2.2. Fire data

We mapped burned patches in ArcGIS 10.0 based on satellite imagery (Landsat 5, Landsat 7, Landsat 8, Sentinel-2) downloaded from the earthexplorer.usgs.gov website for the years 2000 to 2017. We used images from March, April and May to delineate the extent of spring fires, and images from October and November for autumn fires. No fires occur in summer (due to frequent rainfalls and lack of dry biomass) and winter (due to snow cover). Images were set to Colour Infrared (channel combination 543 for Sentinel-2 and Landsat 8, 432 for Landsat 5 and Landsat 7) or Natural Colour (432 and 321, respectively) or single bands were used (usually band 5 or 8), depending on which option showed the sharpest contrast between burned and unburned parts. We manually traced all burned patches within the study area, for each year, generating a shapefile to quantify the extent of each fire (Supplement 2). Fresh burns are easily identified by their typical shape (sharp edges, “fingers” created by flames moving in wind direction and interruptions by barriers such as water courses or roads) and their darkness, resulting in a strong contrast with other habitats (Supplement 2). Shapefiles were then converted into raster files with a cell size of 5 × 5 m and the “maximum combined area” cell assignment type, which assigns the cell the value of the largest area within the cell. Raster files were stacked into a layer of fire frequency in the period 2000 to 2017 in a 25 m^2 grid all over the study area. “Time since fire” is given in months to consider the fact that fires occurred both in spring and in autumn. For simplification, the spring 2017 was set as zero, so autumn 2016 would be six months, spring 2016 twelve months, and so on (Table 1).

Table 1
An explanation of the habitat parameters and their units used in this study.

Habitat parameter	Unit	Explanation
Shrub cover	%	Estimated cover of shrubs (>100 cm height)
Shrub height	cm	Estimated mean height of shrubs (>100 cm height)
Dwarf shrub cover	%	Estimated cover of dwarf shrubs (<100 cm height)
Dwarf shrub height	cm	Estimated mean height of dwarf shrubs (<100 cm height)
Grass cover	%	Estimated cover of grasses (Poaceae/Cyperaceae)
Grass height	cm	Estimated mean height of grasses (Poaceae/Cyperaceae)
Herb cover	%	Estimated cover of herbaceous vegetation
Herb height	cm	Estimated mean height of herbaceous vegetation
Litter cover	%	Estimated cover of dead organic matter
Litter height	cm	Estimated mean height of dead organic matter
Soil cover	%	Estimated cover of bare, unvegetated soil
Moisture		Estimated, between “0” = completely dry to “3” = water-covered
Fire		Fire in the year of study (0 = no, 1 = yes)
Fire frequency		Number of years with fire between 2000 and 2017
Time since fire		Number of months since the last fire

2.3. Bird and habitat data

We compare habitats currently used by territorial individuals (presences) with habitats available to be used (pseudo-absences) (Jones, 2001). First, we mapped presence points of the five study species using the territory mapping approach (Bibby et al., 2000). Points of presence were recorded via GPS marking the exact position where a territory-indicating individual (mostly singing males) of the target species was observed during breeding season between May and June 2017. During this time, we surveyed the entire study area (except for some flooded parts, where our target species are unlikely to occur) by random walks once during the hours from first sunlight until 11 a.m. and only on days with favourable weather (no rain or fog and low winds). Counts were conducted during peak breeding season; thus, bird activity of all species was generally high and the probability to include migrant individuals very low. All presences were included for RB, YB, and CB, while only randomly selected presences of BB and OB were sampled due to their very high abundance within the study area (several hundreds of breeding pairs, see Richter et al., 2020). We included a total of 476 presence points of the target species (BB: 110, CB: 49, OB: 127, RB: 49, YB: 141, for distribution see Supplement 3).

Additionally, we collected habitat parameters at 231 pseudo-absence points spread randomly over the study area (19 of the initially 250 generated pseudo-absence points were removed as they were inaccessible or on agricultural fields). A habitat map for the study area based on a remote-sensing classification (Richter et al., 2020) was used to randomly distribute 35 points within each of the following six habitat classes: shrub, steppe, forest, wetland, reeds and field, adding up to 210 random points. An additional 40 random points were created (irrespective of habitat class) within the recently burned patches to ensure a sufficient coverage, since in spring 2017 only about 10% of the study area burned down (859 ha of 8169 ha), and few of the original random points were in the burned patches. The minimum allowed distance between each of the points was set to 30 m to allow for the generation of the intended number of pseudo-absence points within each of the habitat classes, of which “forest” and “reeds” do not cover large enough areas within the study site to allow for a greater distance between points. Given the very high spatial heterogeneity in habitat structure at our site (Supplement 1) and the small size of buntings' core territories (e.g. mean relocation distance of 28 m in YB, W. Heim unpublished data) we assume that the prolem of pseudo-replication is negligible in our sample. All pseudo-absence points were used in the analysis as absences for all species.

We recorded habitat parameters within a 100 m^2 square around all presences and pseudo-absences between 11th June and 3rd July 2017. These parameters included shrub cover, shrub height, dwarf shrub cover, dwarf shrub height, grass cover, grass height, herb cover, herb height, litter cover, litter height, soil cover, moisture and signs of fire (Table 1). All heights (in cm) and percentage cover of vegetation layers were estimated by eye by the observers from the corners of the plot after several trial runs and satisfying synchronization in the resulting estimates. Height as well as percentage cover values below ten were estimated in steps of one, and those above ten in steps of five. The covers of vegetation layers were estimated independent of each other due to possible overlap. Shrubs and dwarf shrubs always had woody parts, while the herbaceous and grass layers did not contain such elements. Burned and dead parts were treated as part of the original plant if they were still attached to it. Reed was treated as grass. Soil moisture was estimated on a scale of zero to three, with zero signifying “completely dry”, one signifying “moist”, two signifying “waterlogged” and three “standing, open water”. Furthermore, we noted whether more than 50% of the study plot burned down in the year of study (fire: yes) or not (fire: no). Bird occurrence was not noted at the time when habitat parameters were recorded to reduce the time needed and, consequently, to minimize the impact of vegetational changes over the season.

2.4. Statistical analysis

The buntings' niche use based on habitat parameters (Table 1) was analysed in separate models for each species using generalized linear models (GLMs) with a binomial link (i.e. logistic regression). Habitat parameters were fitted as the predictors and the presence/absence of the birds was fitted as the response variable. In a first step, we built two univariate models for all variables, one with a linear relationship and one with an additional quadratic term as we expected non-linear relationships. We tested for spatial autocorrelation in all habitat and fire parameters using a Mantel test in R package ade4 (Dray and Dufour, 2007). We built generalized additive models (GAM) in the package *mgcv* (Wood and Wood, 2015) for parameters with significant spatial correlations ($p < 0.05$). We then included the smoothed coordinates of the presences and absences as covariate to these univariate models. For parameters without significant spatial correlations, GLMs were built with the *glm* function. If at least one of the two univariate models for each parameter were significant ($p < 0.05$) when tested (F-test) against a null model, the parameter was used for further multivariate modelling either with the linear or quadratic relationship. If both of the univariate models (the one with a linear relationship and the one with a quadratic relationship) were significant, the one with the lower Akaike information criterion (AIC) was chosen for further multivariate modelling.

All parameters were then fitted into a model containing all variables at the same time. We used the *dredge* function of the *MuMIn* 1.15.6 package (Barton, 2015) to test all different possible combinations of all variables. A *subset* argument, used to force or prohibit specific combinations of parameters within the dredge function, was implemented to exclude strongly correlated variables (those with a Spearman's rank correlation coefficient ≥0.7) (see Supplement 4) from the same multivariate models (Dormann and Kühn, 2009) as well as to prevent second-order polynomic terms to be included without the first-order linear term in the case of unimodally distributed parameters. We set a limit of six variables to be incorporated in the candidate models, which represents a compromise between preventing overfitting (Guisan and Zimmermann, 2000) by allowing for up to three variables in a quadratic relationship to be fitted to the model (since both polynomic terms of that habitat variable are considered) and a higher number of overall different variables when parameters in a linear relationship are used.

Multivariate models were considered equally adequate when the difference of the AIC (ΔAIC) was below two (Burnham and Anderson, 2002). All of the final models were then manually fitted to calculate Nagelkerke's R^2 (R^2_N), a modified generalisation of the coefficient of determination R^2 to allow for discrete models (Nagelkerke, 1991), and AUC (area under the receiver operating characteristic curve), which corresponds to the probability of correctly distinguishing between “signal” and “noise” (Hanley and McNeil, 1982). The variables included in the best models were regarded as the most important for each of the species.

We used the R package spaa (Zhang, 2016) to compute species' niche breadth and niche overlap, based on all habitat parameters that were significant predictors for the occurrence of at least two species in multivariate models. Niche breadth (B) of a species was calculated using the *niche.width* function and Shannon's index, which considers both the abundance and the evenness of the available habitats (Colwell and Futuyma, 1971): $B = -\Sigma_j p_{ij} \log p_{ij}$, where p_{ij} is the proportion of the individuals of species *i* which is associated with habitat parameter *j*. Species-specific mean values for each habitat parameter were used to compute niche overlap between species using the *niche.overlap* function and the Pianka's measure, which ranges from 0 (no habitat features used in common) to 1 (complete overlap) (Pianka, 1973). We calculated niche breadth and niche overlap separately for recently burned (fire in the year of study) and unburned (no fire in the year of study) territories, if a sample size of at least nine territories was available for each category (burned/unburned). Differences between burned and unburned territories were tested using paired Wilcoxon signed rank tests.

All statistics were carried out in R version 3.4.1 (R Core Team, 2021).

3. Results

3.1. Habitat use

We found significant variation in habitat selection between the studied taxa (Fig. 1, Supplement 5, illustrated in Fig. 2). The preferred habitats of the five species differ in all cases at least in one of the habitat parameters. For example, reed bunting differs from black-faced, chestnut-eared and yellow-breasted buntings in shrub cover and herb cover, and from ochre-rumped bunting in grass height (Fig. 1). Shrub cover, shrub height, dwarf shrub height, grass cover, grass height and moisture significantly affected the probability of presence for all five species in univariate models (Supplement 5, Supplement 6). Fire (in the year of study) and time since fire each affected the presence of only one of the species (Supplement 5, Supplement 6). Fire frequency was a significant predictor for presence in three bunting species in univariate models (Fig. 1, Supplement 5, Supplement 6).

Multivariate habitat preference models showed a good fit for all five species (Supplement 7). Shrub cover, grass height, dwarf shrub height and moisture were part of the final models in all five species, whereas herb cover was included in the final models for four species (Fig. 1, Supplement 5).

3.2. Niche breadth and niche overlap

Shrub cover, dwarf shrub height, grass height, herb cover and moisture were important predictors of presence in at least two of the studied species. We therefore selected these five habitat parameters to calculate niche breadth and niche overlap.

We found significant differences in niche breadth among the five species. The black-faced bunting and the yellow-breasted bunting occupied the widest niches, and the reed bunting occupied the narrowest (Fig. 3).

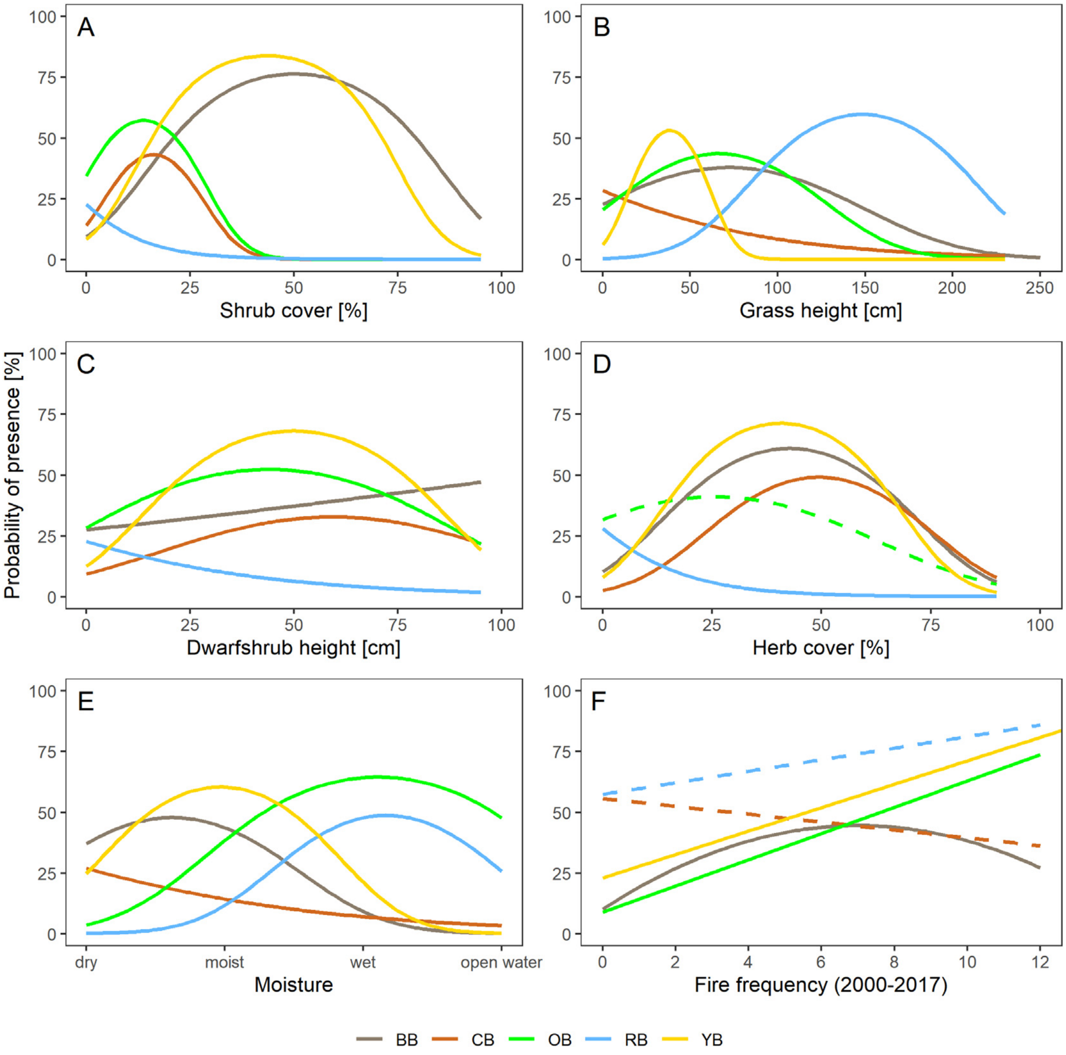

Fig. 1. Probability of presence for five bunting species depending on A) shrub cover, B) grass height, C) dwarf shrub height, D) herb cover, E) moisture and D) fire frequency (number of years with fire between 2000 and 2017) based on univariate generalized linear models with a binomial link. Dashed lines indicate non-significant relationships. BB = black-faced bunting (*n* = 110, CB = chestnut-eared bunting (*n* = 49), OB = ochre-rumped bunting (*n* = 127), RB = (common) reed bunting (n = 49), YB = yellow-breasted bunting (*n* = 141). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

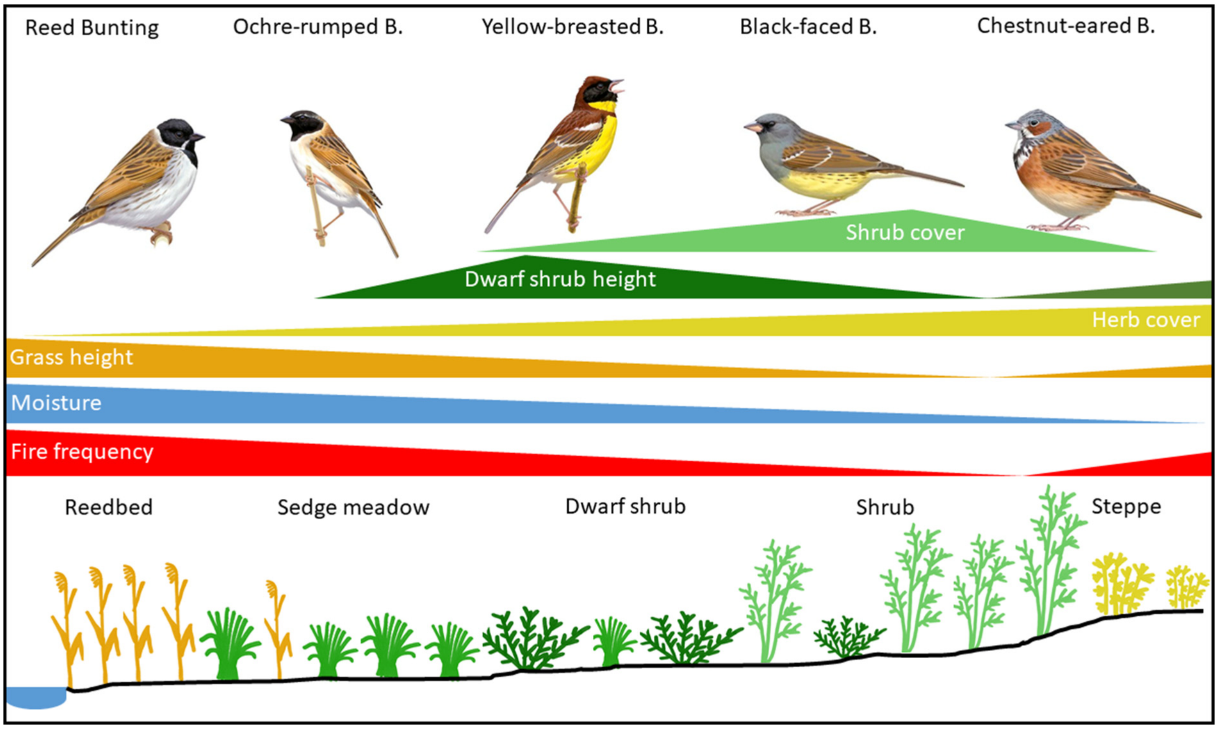

Fig. 2. Hypothetical vegetation characteristics in preferred habitats of the studied bunting species in the floodplain of the Amur River (Russian Far East). Higher bars indicate a presumed stronger use of the referring habitat and habitat structures. Depicted are reed bunting, ochre-rumped bunting, yellow-breasted bunting, black-faced bunting and chestnut-eared bunting (from left to right). Bird pictograms reproduced with permission of © Lynx Edicions.

All species pairings showed high niche overlap of >0.5, apart from those with the reed bunting; here, only the pairing reed bunting/ochre-rumped bunting showed a niche overlap of >0.5 (Fig. 4).

3.3. Fire effects on niche use

We found that niche breadth of all four species with available data (excluding the reed bunting) was lower in burned patches, and these differences were significant in three species (Fig. 3). Niche overlap between the species, however, was only slightly reduced for some species pairings in burned patches, and no significant differences between burned and unburned patches could be found for any of the pairings (Fig. 4).

4. Discussion

4.1. Habitat and niche use

We found high niche overlap in breeding habitat use among five sympatric bunting species (Fig. 4). However, for each of the species pairings, we show that the preferred habitats differ in at least one of the habitat parameters, functionally separating habitats for all species (Figs. 1, 2). The specific habitat preferences as inferred from our models correspond well to descriptions of habitat use for the studied species (Byers et al., 1995).

The reed bunting occupied the narrowest niche and showed least overlap with other species, so we consider it the most specialized species in our

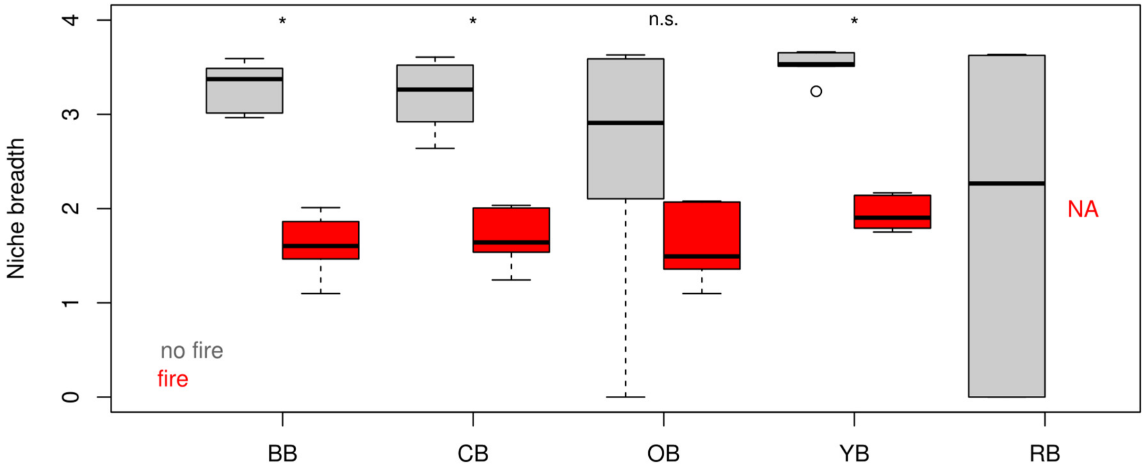

Fig. 3. Mean niche breadth (based on Shannon's index) of five bunting species calculated for five habitat parameters in territories hit by a fire in the year of study ("fire") and from territories which did not burn in the year of study ("no fire"). Boxes represent the lower quartile, median and upper quartile. Species-specific sample sizes (unburned/burned patches): BB = black-faced bunting (74/36), CB = chestnut-eared bunting (40/9), OB = ochre-rumped bunting (109/18), RB = (common) reed bunting (48/1), YB = yellow-breasted bunting (110/31). * = $p < 0.05$, n.s. = not significant.

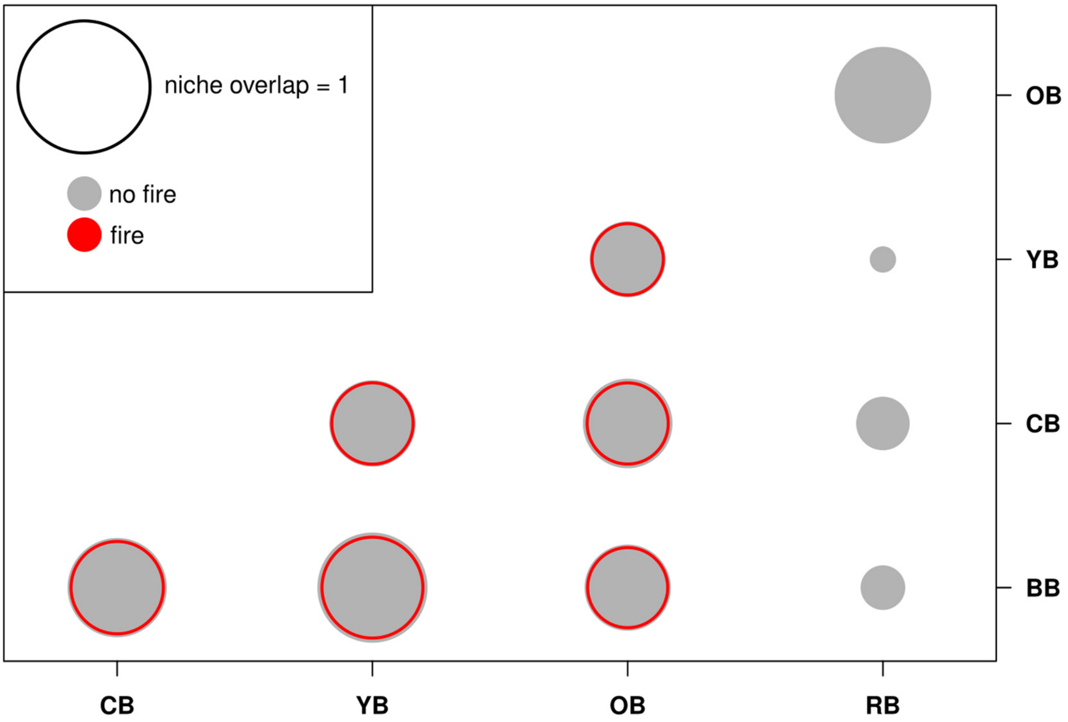

Fig. 4. Niche overlap between all species' pairings based on five habitat parameters from territories that burnt in the year of study ("fire", red circles) and from territories that did not ("no fire", grey circles). Larger circles depict higher niche overlap. If the red and grey circles are of the same size, no change in niche overlap can be expected for a given species pair. Species-specific sample sizes (unburned/burned patches): BB = black-faced bunting (74/36), CB = chestnut-eared bunting (40/9), OB = ochre-rumped bunting (109/18), RB = (common) reed bunting (48/1), YB = yellow-breasted bunting (110/31). Note that insufficient data were available for the reed bunting in burned patches.

study area compared to the other species. All other species occupied wider niches and showed pronounced overlap in niche use and can, therefore, be considered habitat generalists (cf. Levins, 1968).

4.2. Fire effects on habitat and niche use

We found that recent fire was a significant (negative) predictor only for the presence of one species, the reed bunting. However, fire-mediated changes in vegetation structure might affect species' occurrence indirectly (Lyon et al., 2000; Silveira et al., 2016). Most studies on the effects of fire on species assemblages reported changes in the community, with significant differences in species composition and/or abundance before and after a fire event (Fox and McKay, 1981; Fox, 1982; Lyon et al., 2000; Santos et al., 2014; Mérő et al., 2015). Here we present a unique case, in which four out of five species did not show any differences in the probability of presence directly after fire. The fifth species, the reed bunting, clearly avoided recently burned patches, as we found only a single territory in a burned patch. This can be explained by its preferred habitat, reedbeds, a structure that is lost after fire (Mérő et al., 2015), and it confirms our assumption that specialist species with a narrow niche are negatively impacted by disturbance through fire (cf. Kwon et al., 2013).

Fire frequency was a significant predictor of occurrence for three of the species in univariate models. In two species, the probability of occurrence increased with fire frequency. Similar to our study, a positive correlation between abundance and fire frequency was found in a wide range of forest edge species (Moretti et al., 2004). Disturbance through fire creates early successional vegetation stages and, therefore, creates open habitats (White and Jentsch, 2001; Santos et al., 2019), as preferred by the four species showing a positive response to high fire frequencies (Byers et al., 1995). A preference of species occupying open and semi-open habitats for areas with higher fire frequency has also been shown in North American oak savannas (Davis et al., 2000). Populations of such species were also positively influenced by fire in the Mediterranean (Herrando et al., 2002), including a close relative to our study species, the ortolan bunting *Emberiza hortulana* (Brotons et al., 2008). The highest probabilities of presence at high fire frequencies were also recorded for the reed bunting. Although this seems to be in stark contrast with this species' avoidance of recently burned patches, as reported above, since the cover of grasses (including reeds) is known to decrease with increasing fire frequency (Heim et al., 2019), we argue that this species actually does not prefer high fire frequencies but that its preferred habitat is prone to frequent fires. Dry reedbeds provide optimal fuel for fires (Ustin et al., 2009), and all available reedbeds in the study area had burned down more than once during the past 18 years. The only species showing a quadratic relationship with increased fire frequencies, the black-faced bunting, occupies late successional stages such as tall shrubs or open forests (Byers et al., 1995), which only thrive if fires are not too frequent. A preference of later successional stages after fire was also found in a number of shrubland species in Australia (Watson et al., 2012).

Besides direct fire effects, other factors shaping the niche differentiation of the studied species are also driven by fire. For example, shrub cover and grass cover, two of the main predictors for the occurrence of the buntings, have been found to be significantly affected by time since fire and fire frequency, respectively, at our study site (Heim et al., 2019). The height of the vegetation, especially of shrubs, dwarf shrubs and grasses, were also found to describe the niches of our study species. Vegetation height is also affected by recent fire in our study area, either directly or through fire-induced changes in litter cover (Heim et al., 2021). Such indirect fire effects on species' occurrence are also known from other ecosystems (Davis et al., 2000; Rainsford et al., 2020, 2021).

While the studied species seem to cope with fire-induced changes in vegetation structure, we found their niche breadth to be significantly reduced in the year of fire. To our knowledge, this is the first study reporting decreased environmental niche breadths of a set of species after fire. This could be explained by the lack of habitat heterogeneity in recently burned patches, as fires are known to homogenize vegetation structure (Pausas and

Verdú, 2008). The cover of litter and grasses (Poaceae) are significantly reduced after fire in wetlands along the Amur River (Heim et al., 2019), and the removal of litter leads to increased soil temperature (Heim et al., 2021), which could decrease moisture in wetlands. We argue that the limited post-fire structural diversity in the habitats explains the reduced niche breadth after fire; a reduced niche diversity after fire was also observed in insect communities (Swengel, 2001). However, a lack of habitat heterogeneity can also lead to increased niche breadths, but this is only known from dietary niches (Namukonde et al., 2018), not from spatial niches.

Contrary to our expectations, the reduced niche breadth after fire did not lead to increased niche overlap among the species (Fig. 4). We could not detect any significant changes in niche overlap between the species pairs after fire. Negligible differences in niche overlap before and after fire have also been shown for soil arthropods (Pitzalis et al., 2010). We argue that the studied species occupied the same patches before and after fire, leading to similar levels of co-occurrence or competition. This might be connected to high site fidelity in the studied buntings, as reported, e.g., for the yellow-breasted bunting (Bourski, 1996, W. Heim unpublished data). On the contrary, increased niche overlap was found among three species of tree-climbing birds in disturbed sites in Mexico (Lara et al., 2015). However, fire was not the only disturbance in that study, and the difference in niche overlap might be linked to effects of grazing and logging.

Our results suggest that four of the studied buntings show high resilience in maintaining their occurrences after a recent fire. Yet, beyond territory occupancy, the species might show negative responses to recent fires (although not investigated here), such as reduced breeding success in burned patches due to lack of coverage for hiding nests (Pons and Prodon, 1996). As we have mainly sampled the habitat around song-posts of male birds, changes in occurrence at feeding/breeding or female habitats after recent fire might remain undetected. However, for most of the studied species, male song-posts are known to be very close (10-30 m) to the nest locations (Nakamura et al., 1968).

Overall, fires play a critical role for providing open and semi-open habitats for the studied buntings. The occurrence of the species and the structure of the bunting community and their niches are determined by fire frequency. Thus, to sustain populations of all five species, a mosaic of sites with different fire frequencies should be maintained. For yellow-breasted and ochre-rumped buntings, fire return intervals of 1.5 years could increase the probability of presence, whereas an interval of 3 years might be optimal for black-faced bunting (Fig. 1). On the other hand, areas protected from frequent fire might benefit the occurrence of reed bunting.

4.3. Conclusions

We confirmed that anthropogenic fires have the potential to alter bird communities. Niche breadth was significantly reduced after recent fire, but niche overlap between the studied species did not increase. While species' occurrence was not affected by recent fire in the majority of the studied species, we identified fire frequency as one of its major determinants. We argue that investigating fire effects on niche breadth and niche overlap will help to understand changes in the occurrence of species' and communities.

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CRediT authorship contribution statement

Wieland Heim: Conceptualization, Methodology, Formal analysis, Investigation, Writing – Original Draft, Funding acquisition, Project administration; **Alexander Thomas**: Methodology, Formal analysis, Investigation, Writing – Original Draft, Funding acquisition; **Isabelle Berner**: Investigation; **Tim Korschefsky**: Investigation, Funding acquisition; **Norbert Hölzel**: Writing – Review & Editing, Supervision; **Johannes Kamp**: Conceptualization, Methodology, Writing - Review & Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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