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Article

On the relative importance of ecology and geographic isolation as drivers for differentiation of call types of red crossbill *Loxia curvirostra* in the Palearctic

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Efforts to understand the process of speciation have been central to the research of biologists since the origin of evolutionary biology as a discipline. While it is well established that geographic isolation has played a key role in many speciation events, particularly in birds, there is ongoing debate about how frequent speciation is in the partial or complete absence of geographical isolation. In the red crossbill *Loxia curvirostra*, good arguments do exist for sympatric speciation processes. In this species, several classes of calls are clustered in distinct groups, so-called 'call types', which mate assortatively. Often, several call types can be found at a single site, breeding and feeding next to each other. It has been hypothesized that red crossbill call types evolved by specialising in extracting seeds from cones of different conifer species. Alternatively, call types might have evolved in temporal geographic isolation. Within Europe, little is known about the distribution of the various call types and preferences for distinct food resources. In this study, we analysed the temporal and spatial occurrence of red crossbill call types in the Palearctic, investigated potential reasons for call-type composition at a site, and compared the occurrence of call types with the fructification of conifers. Call-type composition changed with site and season but hardly with conifer species. With our data, we could localise range areas of twelve different call types, which cannot be explained by conifer species occurrence. Therefore, we suggest that call types evolved in parapatry in most of the northern Palearctic region, and, although contradictory results exist from Iberia, we argue that differentiation might be driven by the same drivers there as well. Additionally, we discuss the potential influence of anthropogenic changes of forest composition and distribution on call types, which offers a unique possibility for future studies.

Keywords: drivers for differentiation, geographic isolation, *Loxia curvirostra*, red crossbill

Introduction

In the history of evolutionary biology, sympatric speciation was first thought to be the norm (Darwin 1859), but geographical isolation was later considered a necessary

component of speciation, particularly in birds (Mayr 1963). However, the idea that speciation can occur in the partial or complete absence of geographical barriers to gene flow has found both considerable theoretical and empirical (Bolnick and Fitzpatrick 2007) support since then. In very few cases, speciation has been convincingly demonstrated to be fully sympatric – that is, without any role of geographic isolation. Well-studied and iconic examples of such speciation, despite the extensive gene flow between coexisting populations, have been found in fish (Schliewen and Klee 2004, Barluenga et al. 2006), plants (Gottlieb 1979, Ramsey and Schemske 1998) and insects (Berlocher and Feder 2002, Drès et al. 2002, Linn et al. 2004). Together, these studies suggest that speciation with limited or no geographical barriers may be quite regular in some groups. In birds, however, the number of possible cases is relatively small (Sorenson et al. 2003, Bolton et al. 2007; see Päckert 2018 for a discussion of the topic). Some seed-eating birds potentially form an exception, with several examples of speciation with limited geographic isolation and an important role of ecological differentiation known, like some tanagers of the genus *Nesospiza* on Tristan da Cunha (Ryan et al. 2007), Darwin finches (*Geospiza*) on the Galapagos Islands (Grant and Grant 1979, Huber et al. 2007), and capuchino seedeaters (*Sporophila*) in South America (Campagna et al. 2017). However, even in some of these examples, it is not known whether speciation took place in real sympatry or began in allo- or parapatry (like allopatry, but without a complete separation of the populations; Coyne and Orr 2004, Bolnick and Fitzpatrick 2007).

One of the textbook examples of ecological isolation is the red crossbill *Loxia curvirostra*, a finch (Fringillidae) living in the whole Northern Hemisphere (Perrins and Cramp 1998). Groth (1988) discovered that the red crossbill can be split into discrete subpopulations, so-called 'call types', which are separated especially by their distinct flight and excitement calls. To a lesser extent, they differ in their morphologic features; bill depth differs strongest among call types (Groth 1993). Birds of different call types often can be found in the same region, breeding next to each other and feeding from seeds of the same tree species (Kelsey 2008). Benkman (1993) suspected a specialisation of each call type in a specific 'key conifer', the tree species its bill is specialised for. Resulting, these call types are often described as ecotypes (Parchman et al. 2016) or ecomorphs (Sewall 2010) which have been suggested/believed to have evolved in sympatry (Benkman 1993).

The life cycle of red crossbills is closely linked to the availability of conifer seeds as their preferred food resource (Newton 1972). All conifers produce varying amounts of cones and seeds each year, with good fructification (cone crop) in some years, so-called 'mast years', and bad fructification in others, so-called 'crop failures'. Due to tree exhaustion, a very bad cone crop is typically followed by a moderate or good cone crop and vice versa (Thies 1996, Newton 2006). Fructification is, amongst others, dependent on site

fertility and climatic conditions (Mencuccini et al. 1995) as well as exertion of the trees. Red crossbills are common in areas with abundant cones and rare in areas with few cones (Reinikainen 1937). They invade areas with good cone crop and are therefore said to live partly nomadically (Perrins and Cramp 1998).

Compared to North America, less is known about the population structure of the red crossbill in Europe. A recent study (Martin et al. 2019) investigated red crossbill calls in the western Palearctic and found at least 18 different call types (named N1–N15, N17, N23 and S2). There are no studies showing that birds of these European call types are specialised in a key conifer. However, as in North America, differences in bill depth were described for birds of some call types (Edelaar and Terpstra 2004, 2008). In Spain, Edelaar et al. (2012) found that calls, morphological measurements and mtDNA of red crossbills differ among forests with different tree species. However, the large variation of calls without distinct call types at the same location in Spain (Martin et al. 2019) and the lack of differentiation of bill depth between some call types in Great Britain (Summers unpubl.) contradict the results of Edelaar et al. (2012). Hence, the question arises whether isolation by ecology is the main driving force for differentiation in the entire western Palearctic or whether differences in call types were formed during geographical isolation and only subsequently, some ecological differentiation developed.

We investigated the two main existing hypotheses of call-type differentiation. The first states that each of the call types is specialised to extract seeds from the cones of a specific key conifer it feeds on (isolation by ecology; Benkman 1993). The occurrence of several call types overlaps spatially, and individuals recognise each other's specialisation by their call type. Each call type should preferably forage on seeds of a specific key conifer. The geographic distribution should more or less coincide with the distribution of this key conifer. The second hypothesis states that call types are temporally geographically isolated populations, which implies the existence of so-called 'core breeding areas' in which the different call types mainly reside (Dickerman 1987, Knox 1992). The idea of the latter hypothesis is that call types evolve within a geographically restricted 'core breeding area'. During a cone crop failure in this core breeding area, individuals leave for one year, stay and breed somewhere else, and return afterwards. The presumed reason for returning is the likelihood of a good cone crop in the core breeding area in the following year, while the invaded area will likely have a bad cone crop for the same reasons. Therefore, the latter hypothesis implies temporary spatial isolation. It is also possible that a combination of both hypotheses explains differentiation within red crossbills.

To distinguish between these two hypotheses, we collected data on the food resources of the different call types of the red crossbill in Europe, and compared them with spatial and temporal patterns of occurrence of call types. If isolation by ecology and therefore specialisation in a key conifer is the

main driver for the differentiation of call types, we expected conifer species to predict call type distribution. Their geographic distribution should more or less coincide with the geographic distribution of their key conifer. Within a geographical region, the number of call types should not exceed the number of tree species present. In contrast, if call types differentiate by geographical isolation, we expect to find small restricted, non-overlapping areas in which a specific call type is usually very common. These areas should not or only by chance coincide with the distribution range of conifer tree species.

Material and methods

Recordings and classification

We collected 12 805 recordings of red crossbills across the Palearctic region, recorded between June 2010 and May 2018. The recordings were made in 46 different countries, and we received them from different sources (Supplementary material Appendix 1 Table S1). For each recording, we collected its location and recording date. Furthermore, we assigned the calls to the different call types (N1–N15, N17, N23, S2) described in Martin et al. (2019) as well as four additional call types (E1–E4; Supplementary material Appendix 1 Fig. S1, Section 10.2). In each recording, we estimated the minimum number of calling individuals by looking for temporally overlapping calls and distinct frequency or amplitude patterns of the different individuals (detailed method described in Martin et al. 2019).

The most important food resources of red crossbills in Europe are seeds of *Picea abies* and *Larix* spp. (Glutz von Blotzheim and Bauer 2001). We assigned each recording to a 'crossbill season' (as in Newton 2006 or Alonso and Arizaga 2011) which begins with the onset of the coning cycle (Hölzinger 1997), typically in June or July (Thies 1996) and ends in the next spring, typically in May, when the cones open and seeds fall down and are lost for the red crossbills. During a cone crop failure in an area, red crossbills leave it in search of new feeding grounds in the early summer months with the beginning of the new coning cycle. Therefore, we defined a crossbill season as starting in June, when new-generation seeds are available in conifers and ending in the end of May of the subsequent year, when most seeds of *Picea abies* and *Larix* spp. have fallen and red crossbills might be forced to move to another area with more abundant food.

Food preferences and site fidelity of different call types

In search of potential differences in the food resources of call types of the red crossbill, we evaluated decisions of birds to feed on a specific tree species. One of us (JR) noted the tree species in which individuals foraged during fieldwork in France. Red crossbills, like other members of the Fringillidae, visit drinking sites several times a day (Glutz von Blotzheim

and Bauer 2001) and often switch between different trees while feeding (own observations). We cautiously considered only data about the food resource of the same call type taken at the same site if gathered on different days. This surely implies independent decisions to feed on these tree species. If recordings were made on the same day, we only retained a single recording when multiple recordings were made within 500 m of each other (we chose this distance to exclude mistakes which could occur due to inaccuracies of the location data). In case the distance between two recordings taken on the same day of the same call type was smaller than 500 m, we used the recording with the largest number of individuals of the analysed call type. To account for geographic variation in the availability of tree species and test for differences in food resources, we divided the study area into five regions with similar tree species and tested these regions separately (see Supplementary material Appendix 1 Table S2 for more details about these regions). We used data from the seasons 2013/14–2017/18 and of all call types with at least 150 decisions to feed on a specific tree species in the data set. Tree species with less than ten decisions of red crossbills to feed their seeds were removed.

To investigate what influenced the composition of red crossbill call types to feed on seeds of a specific tree species, we fitted a generalized linear mixed model (GLMM; Baayen 2008) with binomial error structure and logit link function (McCullagh and Nelder 1989) in R (<www.r-project.org>), using the function 'glmer' of the R package 'lme4' (Bates et al. 2015). We fitted one such model for each call type. The response variable consisted of the number of decisions of the respective call type to feed on a certain tree species and the number of the other call types to feed on the same tree species. In R, such a response variable is included as a two-column matrix with the number of decisions of the selected call type and the other call types in favour of a given tree species. The key predictors in this model were the random intercept of tree species and the random intercept of site. These model the variation in the probability of occurrence of a given call type dependent on tree species and site; that means, the random effect of tree species will reveal significance when a certain call type preferably occurs in particular tree species and the random effect of site will reveal significance when a certain call type preferably occurs in a particular area. To control for potential differences among seasons with regard to the overall frequency of occurrence of a given call type, we included recording season as an additional random effect. Furthermore, we included the interaction between tree species, site and season as a random effect ('observation level random effect') to test the possibility that the preferences of certain call types for certain tree species vary among sites and/or seasons. As an overall test for the influence of tree species and site, we used a permutation test (Adams and Anthony 1996, Bolker 2008). To this end, we randomized the response within seasons and used the sum of the estimated contribution of the two random effects (standard deviations estimated for tree species and site) as a test statistic. We conducted 1000 permutations into which we

included the original data as one permutation and determined the p-value as the proportion of permuted data sets revealing a test statistic at least as large as the original data. If this test reveals significance, the occurrence of a given call type in certain sites and/or tree species is not random. To test the significance of the individual random effects of site and tree species, we compared the full model with two different reduced models (each with one of the two random effects tree species/site removed), using a likelihood ratio test (Dobson 2002). p-values were adjusted following Bolker et al. (2009). Note that this test is conservative (Bolker et al. 2009; R function 'anova' with 'test' set to 'Chisq'). We checked for overdispersion of the models, which was not found to be an issue (range of dispersion parameters: 0.08 and 0.19 for the different call types). Model stability was assessed by comparing the estimates obtained from a model based on all data with those obtained from models with the levels of the different random effects excluded one at a time (Nieuwenhuis et al. 2012). This revealed the effects of the observation-level random effect and the effects of season to be stable in the model but revealed some uncertainty about the effects of tree species and site Supplementary material Appendix 1 Table S3). The sample for these models consisted of 4253 decisions of individuals to feed on seeds of certain tree species (Supplementary material Appendix 1 Table S4 for more details about the sample size). Call types included N2, N3, N4, N7, N8, N10 and N11, recorded at five different sites (northwestern France, Morvan mountains, Massive Central, French Alps and eastern France (including the Black Forest)), in five different seasons (2013/14, 2014/15, 2015/16, 2016/17, 2017/18), and feeding in seven different tree species (*Abies alba*, *Larix* spp., *Picea abies*, *P. sitchensis*, *Pinus nigra*, *P. sylvestris* and *P. uncinata*). We are aware that fitting a random effect for site with only five levels will lead to the assessment of its contribution to be not very reliable. However, fitting its effects as a fixed effect would lead to a highly complex model which would be likely even less reliable.

Comparison of call-type number with conifer-species number

In a further analysis, we compared the number of call types within a region with the number of occurring conifer species in the same area. If call types differentiated in response to differing cone structures of the tree species, the number of call types should not exceed the number of tree species present. In their study area (north of 25°N and west of 60°E), Martin et al. (2019) found at least 16 (perhaps 17) call types of red crossbills north of 44°N and at least one additional call type south of 44°N. We compared call type number in both areas with the number of regularly present conifer species. For information about conifer distribution, we used the maps published in Andersson (2005), Farjon and Filer (2013), San-Miguel-Ayanz et al. (2016) and American Conifer Society (2017). Additionally, we evaluated information about which tree species red crossbills do and do not forage on, as given in

Perrins and Cramp (1998), Glutz von Blotzheim and Bauer (2001) and Clement and Christie (2017).

Localization of call types' core breeding areas

Differentiation following geographical isolation should be recognizable in a spatial analysis of call-type occurrence data. We evaluated our data (see Recordings and classification) in a grid with 2° of resolution in northern–southern and eastern–western directions within the World Geodetic System 1984 (WGS84). Within each grid cell, we counted the number of individuals of each given call type (18 call types of the red crossbill described in Martin et al. 2019 and four additional call types (Supplementary material Appendix 1 Section 10.3)) that were present, as well as the total number of red crossbills recorded and calculated the quotient of both. For each grid cell, the number of crossbill seasons with available sound recordings was noted, as a high proportion of a call type during several seasons is more indicative for a core breeding area than data from a single season (due to irruptions, call types might be outnumbered by other call types in individual seasons). Our data are well distributed over Europe's western half, fragmentary in eastern Europe, and there are only some data points in the eastern Palearctic (Supplementary material Appendix 1 Fig. S2). To avoid multiple sampling of the same individual, we only used recordings which were separated from all others of the same call type by at least two kilometres or, in case they were made within smaller distances, when more than 100 d elapsed between them (red crossbills take about 39–47 d from nest building to fledging (Glutz von Blotzheim and Bauer 2001)). If there were several recordings of the same call group within this geographical distance (2 km) and time span (100 d), we used the one with the largest number of individuals (same method as in Martin et al. 2019). A core breeding area was defined as a single limited area, where a selected call type was present with a proportion of more than 25% of the red crossbills for more than one season. Data were visualized and checked for potential core breeding areas. Additionally, we compared European conifer-species distribution with the presumed core-breeding and invasion-areas for similar distribution ranges.

Relationship of conifers' seed production within the presumed core breeding area and the occurrence of the respective call type in the invasion area

We analysed the relation between fructification within the presumed call types' core breeding area and the occurrence in the presumed invasion area of the respective call type. We collected conifer fructification data in Europe (Supplementary material Appendix 1 Table S5 for the sources) and compared these with call-type distribution data determined as described in 'Localization of call types' core breeding areas'. Red crossbill occurrence data from May, June and July were excluded as this is the typical period for movements of red crossbills and it is not possible to know whether birds are leaving an area and therefore should be counted for the previous season

or whether they are arriving and should be counted for the next season. The fructification extent was divided into the four categories (Supplementary material Appendix 1 Table S6) used by the ICP (International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests; <www.icp-forests.net>). We only used data of trees older than 35 years, as younger trees rarely have a good cone crop (Philipson 1990) and are rarely utilized by red crossbills for foraging (pers. obs.). To obtain a polygon of the core breeding and invasion area of each call type, a Kernel-Analysis with the package 'adehabitatHR' (Calenge 2006) for R was used. Within the presumed core breeding area (data within the 50% kernel), we searched for available data of conifer fructification. Fructification data were only available for the presumed core breeding areas of three call types (N1, N7, N11) for more than two seasons. We compared these fructification data with the occurrence of the respective call type in its invasion area (75–95% Kernel). To account for varying recording effort, we did not use total numbers of recorded birds but used the ratio of the selected call type of all call types within its invasion area in a given season.

We tested for the relation between fructification within the core breeding area and the occurrence within the invasion area (Supplementary material Appendix 1 Fig. S3) using a generalized linear mixed model (GLMM) with a binomial error structure and logit link function. We included fructification and call type (factor with three levels) as fixed effects in the model. An observation-level random effect (i.e. the combination of season, call type and area) and season were included as random effects. The response was a two-column matrix with the total number of individuals of the selected call type and of the remaining call types, respectively. In essence, this models the proportion of individuals of the respective call type in the invasion area (Baayen 2008). Due to the low number of available data points (seasons with fructification data available: N1: 2011/12 to 2017/18; N7: 2011/12 to 2017/18; N11: 2011/12 to 2014/15; n = total of 18 seasons), we did not include each tree species' fructification as a fixed effect. Rather, we first reduced the number of variables for the model and combined *Larix* spp. (combination of *Larix decidua*, *Larix kaempferi* (Japanese larch), Hybrid-larches and 'unknown' larches (*Larix* spp.) due to difficulties with identification) fructification data with that of *Picea abies* to create a mean fructification index (only this reduced tree species set was used, as these species are the most important food resources of red crossbills in central Europe (Glutz von Blotzheim and Bauer 2001)). For each season, we calculated the fructification index for each core breeding area of the three tested call types.

The model was implemented in R (ver. 3.3.2, <www.r-project.org>) using the function 'glmer' of the package 'lme4' (Bates et al. 2015). We determined the R²-value using the R-package 'MuMIn' (Barton 2016), following the method of Nakagawa and Schielzeth (2013). We checked the model for overdispersion (dispersion parameter 0.43) and also for the distribution of the best linear unbiased predictors (BLUPs; Baayen 2008); both were not an issue. Model stability was assessed by comparing the estimates obtained from a model based on all data with those obtained from models with the levels of the random effect 'season' excluded one at a time. This revealed the model to be stable (Supplementary material Appendix 1 Table S7). To rule out collinearity, we determined variance inflation factors (VIF, Field 2005) using the function 'vif' of the R-package 'car' (Fox and Weisberg 2011) applied to a standard linear model excluding the random effects. This indicated that collinearity was not an issue (maximum VIF: 1.17). p-values for the individual effects were based on likelihood ratio tests comparing the full models with respectively reduced ones (Barr et al. 2013; R function drop1). In a second step, we fitted a model to include the interaction between the mean fructification of *Picea abies* and *Larix* spp. We presumed this to be more realistic as red crossbills often switch to another tree species if seeds of one tree species are not available (M. Marquiss and Rae 1994, unpubl.). However, due to the low number of data points, the power of the model is low. Further, the model's dispersion parameter was 2.07 which means the model is anti-conservative. Hence, the results of this model should be treated cautiously. Again, we checked for model stability and the model was shown to be stable (Supplementary material Appendix 1 Table S8). To rule out collinearity, we determined VIF (for calculation of the VIF, we excluded the random effects and the interaction); this did not indicate collinearity to be an issue (maximum VIF: 1.91).

Results

Food preferences and site fidelity of different call types

The relative frequency of occurrence of call types varied among tree species and among sites (permutation test; full null model comparison significant in all call types except N4; Table 1). Therefore, we tested tree species and site for their individual effects in the remaining models: call type occurrence was predicted by site (significant in five out of six call types; Table 1). Three call types preferred specific tree species (significant results for N3, N10 and N11; Table 1), however, these preferences changed among seasons and/or sites (significant observation-level random effect in all three call types; Table 1). For instance, N11 fed mainly in *Pinus mugo* in 2015/2016 but in 2016/2017 especially in *Picea abies* (Fig. 1).

Comparison of call-type number with conifer-species number on a local scale and comparison of distribution ranges

North of 44°N and west of 60°E, seven native coniferous species occur on which red crossbills forage regularly (two species of larch (*Larix decidua*, *L. sibirica*), three species of pine (*Pinus mugo*, *P. sibirica*, *P. sylvestris*), and two species of spruce (*Picea abies* and *P. obovata*); red crossbills only forage on *Pinus cembra* when cones are open (Glutz von Blotzheim

Table 1. Summary statistics of the GLMM including 'conifer species', 'site', 'season' and 'observation level' as random effects.

Call type	Test of site and conifer species (full-null model comparison)		Random effect: conifer species			Random effect: site			Random effect: season			Random effect: observation level		
	Test statistics	p-value	χ^2	df	p adj.	χ^2	df	p adj.	χ^2	df	p adj.	χ^2	df	p adj.
N2	2.76	**0.01**	0.46	1	0.25	91.08	1	**0.001**	<0.001	1	0.50	0.46	1	0.25
N3	1.68	**0.05**	30.54	1	**0.04**	0.37	1	0.27	0.22	1	0.32	30.54	1	**0.04**
N4	1.69	0.07	0.00	1	0.50	237.55	1	**<0.001**	81.50	1	**<0.01**	<0.001	1	0.50
N7	2.53	**0.04**	0.24	1	0.31	176.88	1	**<0.001**	21.65	1	0.07	0.24	1	0.31
N8	1.80	**0.02**	12.74	1	0.13	41.07	1	**0.02**	<0.001	1	0.50	12.74	1	0.13
N10	6.62	**0.02**	40.25	1	**0.02**	211.45	1	**<0.001**	61.91	1	**<0.01**	40.25	1	**0.02**
N11	2.12	**0.01**	62.12	1	**0.01**	50.45	1	**0.01**	126.21	1	**<0.001**	62.12	1	**<0.01**

and Bauer 2001)). Seven additional coniferous species have been planted in large areas within the last five hundred years (*Larix kempferii*, *Picea sitchensis*, *Pinus contorta*, *P. nigra*, *P. pinaster*, *P. strobus* and *Pseudotsuga menziesii* (Farjon and Filer 2013, San-Miguel-Ayanz et al. 2016, EUFORGEN 2019).

In total, at least 17 call types of the red crossbill occur in the same geographical area, where red crossbills were found to forage on 14 or less tree species on a regular basis (we have no information whether seeds of *Pinus pinaster* are consumed by red crossbills).
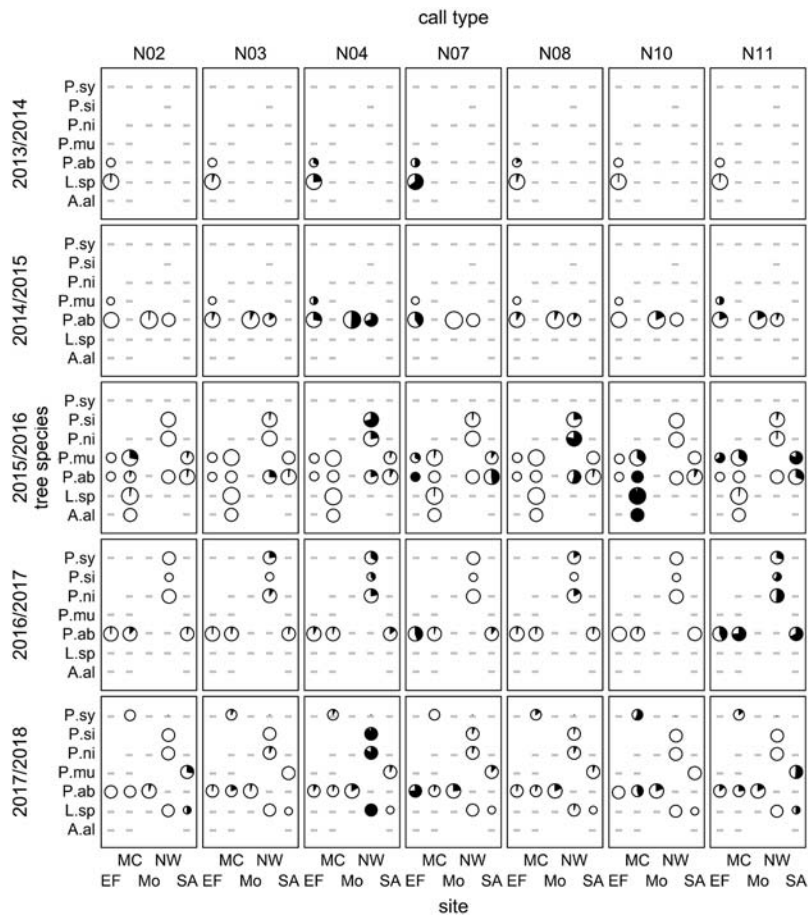

Figure 1. Proportion (black sector of the circles) of call types (columns) feeding in a conifer species (y-axes) at different sites (y-axes) in different seasons (rows). The area of the circles is proportional to the logarithm of the number of available decisions to feed or not feed on these conifers. P.sy = *Pinus sylvestris*, P.si = *Picea sitchensis*, P.ni = *Pinus nigra*, P.mu = *Pinus mugo*, P.ab = *Picea abies*, L.sp = *Larix* spp., A.al = *Abies alba*, EF = eastern France (including the Black Forest), MC = massive central, Mo = Morvan Mountains, NW = NW-France, SA = south-western Alps. See Supplementary material Appendix 1 Table S2 for information about these areas and the occurring conifer species. We had no zeros in the dataset, however, as data were collected opportunistically at different sites, missing data also hint to an absence of any call types in the respective conifer species. An empty field means, the conifer species was not available at the recording sites.
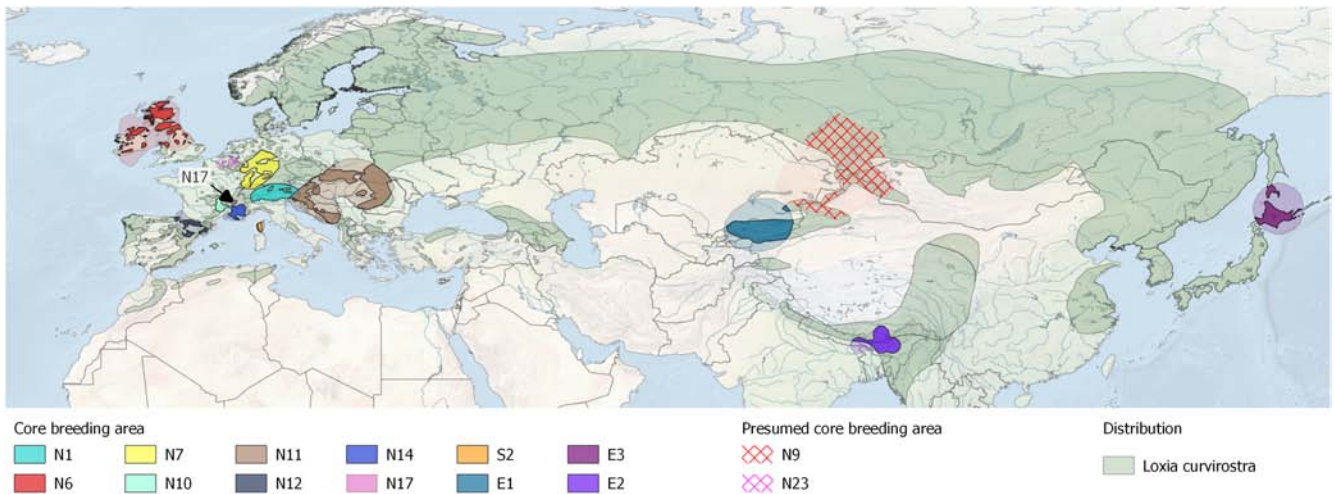
Figure 2. Core breeding areas and presumed core breeding areas of the call types of the red crossbill in the Palearctic region. The core breeding areas were determined with a Kernel-Analysis in R. Within these Kernels, the overlap with the range of the red crossbill is highlighted. Distribution data are from BirdLife International and Handbook of the Birds of the World (2017). Maps are from Natural Earth (2018).

South of 44°N and west of 60°E, 15 coniferous tree species visited by red crossbills for foraging grow on a regular basis (*Picea omorika* occurs in a very small area, *P. abies, P. orientalis, Pseudotsuga menziesii* and *Larix decidua* are just spread in small areas as well; additionally, there are *Pinus brutia, P. halepensis, P. mugo, P. nigra, P. peuce, P. pinaster, P. pinea* and *P. sylvestris* (Andersson 2005, Farjon and Filer 2013, San-Miguel-Ayanz et al. 2016)). Red crossbills also occasionally forage on *Cupressus sempervirens, Cedrus libani* (Glutz von Blotzheim and Bauer 2001) and *C. atlantica* (unpubl.). We do not know whether *Pinus heldreichii* is also used for foraging. We found many different call variations south of 44°N, most just present within a very limited area (Martin et al. 2019) not coinciding with tree-species distribution. Six call types occurred north and south of 44°N, and only two call types occurred only south of 44°N (S2, found only on the isle Corsica, and S8, uttered by a low number of individuals). Hence, tree-species number exceeded distinct red crossbill call types by far in the southern study area (but at the same time, it was hardly possible to put a number on the extensive call variation).

When comparing distribution ranges of call types and tree species (10.4), we had no sufficient data for 7 of the 22 analysed call types. For one call type (N1), distribution range roughly matched the distribution of a conifer species (*Pinus mugo*). The distribution of the remaining call types resembled only slightly, if at all, the distribution of the conifer species in the study area.

Localization of the core breeding area

We found small restricted areas with a high proportion of the respective call types, present over several seasons for 12 out of the 22 analysed call types (N1, N6, N7, N10, N11, N12, N14, N17, E1, E2, E3 and S2; Fig. 2 and Supplementary material Appendix 1 Fig. S4–S25, as well as 4.3). Sometimes,

more than 50% of the local birds belonged to the same call type during the whole study period. For two further call types (N9 and N23), hints for a core breeding area were found, but for these sufficient data were not available for conclusive evidence. In our data set we found four additional potential call types that were not described in Martin et al. (2019: E1–E4, see Supplementary material Appendix 1 Section 10.2).

Relationship between conifers' seed production within the presumed core breeding area and the occurrence of the respective call type in the invasion area

Relative abundance of each tested red crossbill call type in its invasion area (Fig. 3) was negatively correlated with mean fructification of *Larix* spp. and *Picea abies* in its core breeding area (Fig. 3; likelihood ratio test: $\chi^2 = 18.05$, df = 1, p < 0.001). Conditional and marginal R^2 showed that 27% of the variation was explained by the fixed effect and 29% by the entirety of fixed and random effects. In the model including the interaction between the fructification of *Picea abies* and *Larix* spp., it was confirmed that red crossbills switched between different conifer species (Supplementary material Appendix 1 Fig. S26; likelihood ratio test: $\chi^2 = 16.48$, df = 1, p < 0.001). Occurrence in the invasion area was especially pronounced when both tested conifer species had low cone crops. The effect size for the model including the interaction was much higher ($R^2 = 0.61$ for the fixed effects as well as for the entirety of fixed and random effects).

Discussion

We found evidence that geographical region predicts occurrence of red crossbill call types better than tree species in Europe. Amongst others, we found more call types than tree species in the western Palearctic north of 44°N. This excludes a
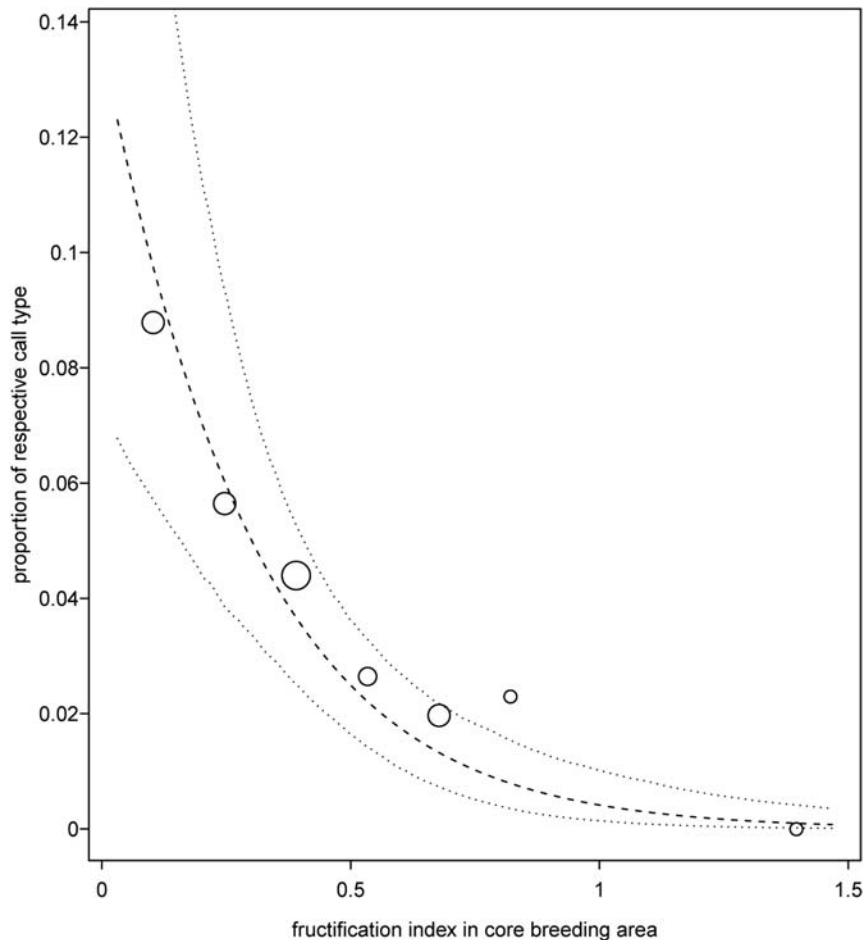
Figure 3. Occurrence of the call types N1, N7 and N11 in their respective invasion area in dependency of the fructification (a higher fructification index means more cones, see Supplementary material Appendix 1 Table S6) of *Picea abies* and *Larix* spp. in their respective core breeding area. The dashed line depicts the fitted model and dotted lines show the respective 95% confidence limits. The area of the dots is proportional to the amount of data points.

one-to-one specialization of individuals belonging to different call types in a particular tree species. Furthermore, in France, we found that the sampled site had the strongest influence on call-type composition, while the available tree species had only a minor influence. The preferences for certain tree species even changed between different seasons/sites for the same call types. A spatial analysis confirmed the existence of so-called core breeding areas (regions where a certain call type mainly resides). Fructification of spruce and larch in these core-breeding areas predicted call type occurrence elsewhere. All found core breeding areas were geographically separated from each other (two overlapped in a small area). Fructification of *Picea abies* and *Larix* spp. in the tested core breeding areas predicted call type occurrence in their invasion area.

What is driving call-type differentiation in the red crossbill?

In the western Palearctic north of 44°N, the number of call types (17) exceeded the number of regularly occurring conifer species (14) in which red crossbills feed. This ruled out a

one-to-one specialisation of call types in tree species. In addition, the potential for a one-to-one specialisation is reduced by the fact that the differences between the cones of some tree species are very subtle and hybrids between tree species are common in some conifer species (e.g. *Picea* x *fennica* in northeast Europe (Farjon and Filer 2013); *Larix* x *eurolepsis* in Scotland and Switzerland (San-Miguel-Ayanz et al. 2016)). This further increases the overlap in cone structure. In the western Palearctic south of 44°N, tree species' number (15) exceeded the number of call types (7), but this could not explain the extensive and partly clinal call variation in this area (only seven different call types were present, most were rare and much more frequent north of 44°N, suggesting a northern origin). Our interpretation that red crossbill call types are not specialized in extracting seeds of specific conifer species' cones was further supported by the results of the analysis about food preference and call-type location fidelity in France: call-type preferences for specific conifer species changed between seasons and/or sites, which might indicate a preference for the easiest accessible food at a specific site in a season or the best input–effort ratio (Glutz von Blotzheim

and Bauer 2001, Broome et al. 2016). It can be argued that fructification extent or seasonal changes in food choices may mask the effects of ecological specialisation. However, differentiation is less likely if the selection pressure is maintained only for a fraction of the time (otherwise it would have to be visible in the data) and the other arguments presented remain. In summary, we conclude that both, the comparison of the number of conifer species and call types and the results of the analysis of call-type food preferences in France provide no evidence for a specialisation to a key conifer. A further argument against specialisation to a key conifer is the bill measurements of the different call types. Bill depth was shown to be the most differing morphological feature of two call types (Edelaar et al. 2008). Nevertheless, bill depth between these call types is widely overlapping, and sex affected bill measurements in some cases more than call type (Edelaar and Terpstra 2004, Edelaar et al. 2008, Summers 2020). If these small differences in bill size have a negative effect on fitness, this would imply that males and females have specialized in different tree species. However, they commonly feed next to each other (unpubl.). Between other call types, no differences in bill depth were found – only in wing length (Summers 2020), which also contradicts a specialization in a specific tree species. The overlapping morphology of bill dimensions also reveals that differing calls of the call types are not driven by differing morphological characteristics, such as in Darwin finches (large-billed individuals use lower frequencies and slower trills; Podos 2001, Huber and Podos 2006).

In fact, we found core breeding areas of 12 call types in the study area (however, for many areas in the eastern Palearctic, not enough data were available for a robust analysis). Hardly any core breeding or invasion areas coincided with the distribution of specific conifer species. However, all core breeding areas were located in more or less demarcated mountainous regions. This can be explained by food availability: differentiation probability within two mobile, only temporarily geographically isolated populations increases with time spent isolated. Transferred to red crossbills, a continuous food supply in the core breeding area is necessary to maximise the time spent in the core breeding area. Conifer fructification is strongly influenced by climate (Röhrig and Gussone 1990). However, in mountainous regions, the microclimate depends on slope and altitude. Although the average fructification decreases with altitude (Mencuccini et al. 1995), mountain regions likely offer more variation in the degree of fructification than lowlands. In addition, altitudinal differences in temperature promote a later seed fall at higher altitudes and thus ensure food availability for a longer period of time. Mountains offer also different conifer species in different elevation, which further increases the chance that food is available in an area each season (Broome et al. 2016), as some conifer species (e.g. *Pinus sylvestris* (Scots pine; Thies 1996) and *P. contorta* (lodgepole pine; Burns and Honkala 1990)) produce seeds more regularly than others (e.g. *Picea abies* Norway spruce; Thies 1996 and *Larix decidua* European larch), and cone crops of different conifer species are not always synchronous. Mountain areas with several different

conifer species are therefore best suited for a development of call types and can be compared to islands with constant food availability surrounded by lowlands with more irregular food availability. Crossbills remain especially on these 'islands' and are therefore temporally isolated. For few call types (like N3, N4 and N8), we have not found core breeding areas, although we had a lot of recordings. This may be due to the fact that we had insufficient data from the eastern Palearctic, which presumably also hosts core breeding areas. However, it is also possible that there is, additionally, a totally nomadic population of red crossbills. In summary, our data suggest that at least most call types represent geographically clustered populations.

The results of our study are partially in line with and partially contradict publications from North America, where Benkman (1993) suggested that each call type is specialized in a particular conifer species. However, he also suggested that they might not be very faithful to any given resource during most of the year, when food is plentiful, but that resource specialization, divergent selection and population divergence might occur when food is scarce. In Europe, cones of most conifer species (*Larix* spp. and *Picea* spp.; Thies 1996) contain seeds in autumn, winter and spring. Food availability and accessibility is probably worst in late spring and early summer, but many red crossbills switch to pine (*Pinus sylvestris, P. mugo, P. nigra*; Bijlsma 1994; Thies 1996; Glutz von Blotzheim Bauer 2001, own data) at this time of the year. The number of tree species to which red crossbill call types could differentiate would thus be even lower. The discrepancy between call-type invasions and core breeding areas with the distribution of conifer species in the western Palearctic does not fit this hypothesis – neither does the higher total number of call types than tree species in the western Palearctic north of 44°N. In line with our results, Kelsey (2008) could not find a preference of call types for a single conifer species in North America when analysing the spatial composition of call types at the local level. Different call types all fed on the same conifer species, although different conifer species had plenty of cones, including the proposed 'key conifers' of some of the call types. Instead, he found a large spatial separation of the different call types, as we found in our study. He suggested that differences in beak dimensions were an adaptation to a resource class (a group of conifer species most abundant in the core breeding area). In sum, findings in North America are inconclusive and further research is needed to clarify whether geographical isolation or isolation by ecology drives red crossbill differentiation in North America.

In the western Palearctic, the situation south of 44°N differs considerably from the situation north of 44°N with only one distinct call type found, which did not belong to the call types north of 44°N (Martin et al. 2019). The two areas clearly differ in their food resources. In the south, the coniferous forests consist of different *Pinus* species (San-Miguel-Ayanz et al. 2016), which all produce seeds more regularly and reliably than northern species such as *Picea abies* or *Larix* spp. (Harper 1977, Clouet 2000, Tapias et al. 2011; data set from ICP Forests (<www.icp-forests.net>). This reliable

food availability allows the red crossbills to live and feed on these forests throughout the year (Senar et al. 1993) and to move only over short distances (Alonso et al. 2016, SEO BirdLife 2018). Shorter movements favour the development of geographical dialects (Belliure et al. 2000, Catchpole and Slater 2008), and probably, since conifer seeds are more or less regularly available everywhere in the southern forests, the calls cannot be divided into different call types, but vary over distance (confirmed by Martin et al. 2019). These results suggest that the same drivers of differentiation are acting in the western Palearctic north of 44°N as in the south, yet under different circumstances. This result is confirmed by Parchman et al. (2018), who found that red crossbills living in geographically isolated areas with a stable food resource (here *Pinus halepensis*) were genetically distinct from other red crossbills.

In a study of Spanish red crossbills, Edelaar et al. (2012) linked morphology, genetic information and call types in different study areas. They found that the similarity of calls, bill measurements and mitochondrial and nuclear DNA sequences increased in forests with different conifer species, but not with geographical proximity. Based on these findings, Edelaar et al. (2012) argued that isolation by ecology is the main driver for differentiation in red crossbills, in contrast to our results. For the vocal data in this study, it remains unclear whether geographical isolation or isolation by ecology explains the distribution due to the very small sample size of four geographically separated data collection points (with three different pine species included; interpreted as an argument for isolation by ecology). Calls are not necessarily linked to bill measurements and genetics, but the results for differences in the mtDNA and nuclear DNA were also only significant when three out of 14 populations were assigned to another conifer species (reasoned by an inappropriate bill size). The differing results may indicate that the interaction of the driving forces affecting population differentiation differs between the Mediterranean region (with mainly resident populations) and northern Europe (with temporarily nomadic populations). However, we argue that for future research about driving forces in the Mediterranean, a study site with a random distribution of conifer species would be desirable (achievable by using a forest patch with different conifer species present). Ideally, marked birds should be followed for several years (with different fructification rates of different conifer species).

The results of the analysis of call-type differentiation (geographical isolation with temporal overlapping of the different call types) fit the 'stepping stone model' in a parapatric speciation process (Coyne and Orr 2004). It postulates discrete populations with restricted gene exchange and thus enables a differentiation of these populations. Similar differentiation processes are also found in other representatives of the Fringillidae, for whom allopatric (Kirwan and Atkinson 2006), peripatric (Förschler et al. 2009) and parapatric (Ivushkin 2015) differentiation processes are well-known. A parapatric differentiation process very similar to that of the red crossbill has been found for the evening grosbeak *Hesperiphona vespertina* in North America, a close relative of the red crossbill. For this species, five discrete call types of flight calls have been described (Sewall et al. 2016). As with the red crossbill, there are reports that these call types sometimes breed in the same geographical area. However, they are usually more obviously geographically clustered than in the red crossbill. Similar to the red crossbill, the morphological differences of these call types are subtle, and only three subspecies are recognized today (Clement 2018). The evening grosbeak has a similar life history to the northern red crossbills, as it is mostly resident but occasionally migrates long distances (Sewall et al. 2016). Certain aspects of life history appear to influence the structure of the birds' vocal repertoire. Members of the Fringillidae with limited dispersal show well-developed morphological, vocal, genetic and ecological differences, especially when populations are geographically isolated (Marshall and Baker 1999, Förschler and Kalko 2006, Förschler and Siebenrock 2007, Förschler et al. 2009, Garcia-del-Rey et al. 2013). In contrast, some of the most mobile species of the Fringillidae with very low site fidelity (Newton 1972), such as the siskin *Spinus spinus*, show no known call differentiation (nor subspecies; Cramp and Perrincs 1994, Glutz von Blotzheim and Bauer 2001). The calls are no longer population specific, but flock specific. Accordingly, siskin and pine siskin (*S. pinus*) are open-ended learners (Mundinger and Messmer 1970) that are even able to adopt other species' calls. Coyne and Orr (2004) suspected that sympatric speciation is as likely among the most mobile species as among less mobile species. However, the probability of allopatric speciation does decrease in more mobile species (Belliure et al. 2000, Catchpole and Slater 2008). Despite this increased likelihood of sympatric speciation in more mobile species, we are not aware of any study of a European finch that presents arguments in favour of complete isolation by ecology (except the above-mentioned studies on Iberian red crossbills). In summary, among the European Fringillidae, geographic isolation seems to be a needed prerequisite for differentiation, and (at least northern) red crossbills fit well into this pattern.

Reasons for evasions of red crossbills

The reasons for red crossbill evasions (which means an invasion somewhere else), are not fully understood (fructification extent and population size are thought to be the main causes; Newton 2006). While the occurrence of red crossbills within a forest patch correlates with the local fructification of the conifer species (Reinikainen 1937), the reasons for the proportion of different call types within a forest patch are unknown. To our knowledge, this study is the first to attempt a statistical analysis of red crossbill occurrence in an area and cone crop in the suspected area of origin. Newton (1972) tried a similar approach: he discussed red crossbill occurrence in central Europe in connection with conifers' fructification in Sweden. However, he did not have any quantitative data and did not know where the red crossbills that entered central Europe came from. Therefore, he probably did not measure the extent of the cone

crop in the area of origin of the red crossbills responsible for the influx, which may have caused his inconclusive results. In our study, we compared the cone crop in the core breeding areas of three call types with their occurrence in the respective invasion area. Population size was not included in the model, as we had no data about this (we did not know the origin in advance and therefore could not measure population size). We found a negative correlation between the two variables, but with a small effect size. The reason for the small effect size might be that we built the model with large simplifications due to the small number of data points. It is a drawback of our study that we had to work with opportunistically collected data, as it was not possible to collect standardized and continent-wide data over several years on the call type occurrence and the availability of different conifer species and their seeds. Fructification extent would ideally have been assessed by weighing the seeds per cone, as the number of cones is not perfectly correlated with seed availability (Broome et al. 2016; the weight of seeds per cone may vary by a factor of two in *Picea abies* and even more in *Pinus sylvestris*). Other conifer species could have also been included, as red crossbills change between different conifer species over the years (Fig. 1; Marquiss and Rae 1994). As a first step in this direction, we have also created a model with an interaction between the cone crop of *Larix* spp. and *Picea abies*. The change between food resources was confirmed and the resulting effect size of the model was higher than without the interaction. In summary, cone number of *Picea abies* and *Larix* spp. in the core breeding area predicted the occurrence of the respective call type in the invasion area. It probably cannot explain the full extent of the invasions, since population size certainly has an influence as well, but it has likely a greater influence than previously assumed.

How fast can call types differentiate?

A recent analysis of the crossbill (*Loxia* spp.) genome (Parchman et al. 2018) found hardly any differences between some of the northern European red crossbill call types and also between red and parrot crossbills (*L. pytyopsittacus*). This indicates ongoing gene flow, recent differentiation or both. Persistent but low gene flow has been found and is probably already enough to prevent genetic differentiation (one out of 86 pairs with different call types of the mates (own data from France); one out of 38 pairs with excitement calls of another call type and one out of 18 pairs with flight calls of another call type (Scotland; Summers et al. 2007); five out of 407 pairs with mixed calls (North America; Keenan and Benkman 2008). A recent differentiation of call types is likely as well. In Europe, conifer distribution has changed drastically since the last glacial period. The core breeding areas of call types within the Alps (N1, N14 and N17) were covered with ice during the last ice age and there was probably no suitable habitat for red crossbills. In the core breeding area of N7 (southwestern low mountain range in Germany), *Picea abies* immigrated only about 8000 years ago (Latałowa and van der Knaap 2006). Great Britain and Ireland were covered with ice and therefore unsuitable for N6, which occurs

there today. Hence, at least some red crossbill call types are likely to have developed after the last glacial period. With a more detailed look at forest development in Europe, at least some red crossbill call types could represent a much more recent differentiation. The only native conifer species in Great Britain and Ireland is *Pinus sylvestris* (San-Miguel-Ayanz et al. 2016). In these forests, Scottish crossbills (or perhaps parrot crossbills – see the 'preference' of the first for *Pinus contorta* (Summers and Broome 2012)) are considered native (Nethersole-Thompson 1975). Red crossbills reached Britain only during invasions (cf. citation of Matthew Paris, St. Albans 1251 and Wats 1640, in Nethersole-Thompson 1975). The planting of *Picea* spp. and *Larix* spp. started, to a small extent, in Great Britain between the 16th and 19th centuries (*Picea abies* about 1548, *P. sitchensis* in 1831, *Larix decidua* in the early 17th century, Anderson 1967, Davies 1979, Woodland Trust 2020) and increased especially after the 2nd world war in the 1950s (Warren 2009). Since no suitable conifer species grew in Great Britain before the 16th century, N6 probably developed within the last 500 years. Berthold (1992) suggests that regularly occurring crossbills are a very young phenomenon in southern Germany as well (call type N7 occurs there). He presumes it is a consequence of forest dieback (which mainly affects higher altitudes), since trees are more likely to fructify in response to stress. However, he mentions no further data to prove this.

Hints for population differentiation within such a short period of time as shown here is exceptional. Red crossbills, however, belong to the song-learning passerines. Among others, Thielcke (1970) and Lachlan and Servedio (2004) suggested that differentiation of species is faster when songs are learned rather than innate. In fact, Jetz et al. (2012) found higher diversification rates in passerines than in non-passerines. Crossbills learn not only their songs but also their flight calls (Sewall 2010), which are an important prerequisite of assortative mating (Snowberg and Benkman 2007). Crossbills even actively adapt their flight calls during pair formation to those of their mate (Keenan et al. 2008), which could further accelerate differentiation (while simultaneously allowing for gene flow among call types). In summary, the key to this potentially extremely rapid differentiation of call types could be the ability to differentiate vocalisations from other populations in a very short time.

This presumed rapid adaptation to local conditions provides a unique opportunity for future studies on birds' evolution in the Palearctic. In Darwin finches, the establishment of a distinct population was shown to take place within a few generations (Lamichhaney et al. 2018), and differences in body and bill sizes within a population have also been shown to change within one generation in the presence of strong natural selection (Boag and Grant 1981). If red crossbills adapt comparatively rapidly to local conditions, it is likely that forest plantations strongly influence the distribution and evolution of call types. Since the 18th century (Farjon 2017), various species of conifers have been planted extensively in Europe. This may have created suitable conditions for the development of call types, or core breeding areas

of previously separated call types may have been merged. In the second half of the 20th century, climate change shifted the favourable altitudinal range of *P. abies*, one of the most common conifer species in central Europe upwards (Falk and Hempelmann 2013). *Picea abies* also suffered from further factors like diseases and pests (Rehfuess 1985). Additionally, the species proved to be susceptible to the severe storms and droughts of recent decades, due to the flat root system (San-Miguel-Ayanz et al. 2016). It is probably for this reason that *P. abies* is in decline and, at least in the lowlands of central Europe, it will be planted less frequently. This is likely to have an impact on the spatial occurrence of call types and it is unclear whether, for example, call type N7 will survive if in future *P. abies* is restricted to the higher altitudes of central Europe. If *P. abies* is replaced by another conifer species in these areas, N7 might survive but might undergo changes of its bill morphology. Forestry may also promote the development of new call types in the near future if previously woodless areas are reforested. For example, conifers are not native to Iceland, but several conifer species were introduced during reforestation in the mid-20th century. The first red crossbill brood on Iceland was recorded in 1994 (Þráinsson et al. 1995); since 2008 at the latest, red crossbills have been breeding every year on Iceland (Kolbeinsson and Pétursson 2013, Þráinsson et al. 2013a, b, Y. Kolbeinsson unpubl.). Different call types that have reached the island are crammed together in a relatively small area and mostly cut off from other populations. These birds might develop a new call type within a short period of time by call matching or for other reasons. To summarize, we suggest that the composition of the call types within Europe is at least to some extent man-made and could change in the near future. We therefore propose to take advantage of this possibility and start a long-term monitoring of the spatial–temporal distribution of call types, their morphology and genetic differentiation. This will help to get a better understanding of the underlying mechanisms of population differentiation.

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Data availability statement

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.2358> (Martin et al. 2020).

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Supplementary material (available online as Appendix jav-02358 at <www.avianbiology.org/appendix/jav-02358>). Appendix 1.