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Parapatric Genetic Lineages Persist in a Multiply Introduced Non-native Bush-Cricket

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To understand colonization success of an invasive species we need to know the origin of the founders, where and when they were introduced, and how they spread from the introduction site(s) through the landscape. Admixture of different genetic lineages from multiple introductions is generally hypothesized to be beneficial to invasive species thanks to adaptive variation and heterozygosity-fitness correlations. In this study, population genetic and landscape data was gathered for Roesel's bush-cricket, *Roeseliana roeselii* a small bush-cricket common in central and eastern Europe that currently is expanding its range in northern Europe. We examined how colonization history and landscape structure affect the spread of the species and its population genetic structure, as a consequence of multiple introductions. Using comprehensive information of the species ecology and dispersal, together with genetic structure inferred from samples from 29 locations in central Sweden (we employed data published by Preuss et al., 2015), we found that two parapatric founding lineages have coexisted with very little gene flow during a long time span. An isolation-by-distance pattern and a decrease of genetic diversity toward marginal areas were more pronounced in the lineage situated in forest dominated landscapes. Our findings are in strong contrast to the hypothesis that different genetic lineages will admix when introduced to the same area. The presence of the separate lineages decades after introduction and without physical barriers for gene flow shows that some mechanism prevents them from admixture. One possibility is that the lineages with different genetic setups have adapted independently to local conditions and their admixture resulted in loss of locally adapted genotypes and hybrid offspring, less viable than the respective ancestral genotypes. However, an alternative post-mating reproductive barrier and hybrid breakdown phenomenon should also be considered. Our data indicate that besides landscape characteristics, human transportation of agricultural goods may play an important role for the overall spatial genetic pattern of the species in the study area by aiding the spread of the species.

Keywords: human assisted dispersal, landscape connectivity, land-use, microsatellites, Orthoptera

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INTRODUCTION

Different management strategies are used to prevent invasive species from entering new regions, to hinder them from establishing viable populations and expand within an area (Baker, 2017; Liebhold and Kean, 2019). For all these actions, there is a need to understand the ecology of species; e.g., how different traits may increase invasiveness and how the composition of the landscape affects establishment and spread (Beckmann et al., 2015; Fidler et al., 2018; Williams et al., 2021; Wyse and Hulme, 2021). Previous studies have found that species with low movement ability and/or with low adaptation capacity are generally less successful in establishing in new areas (Wamser et al., 2012; Medley et al., 2019). Fragmented landscapes where habitat patches are far apart and dispersal barriers are common, also impact the success of colonization and can hinder or slow down the spread of species (Greenwald et al., 2009; MacDonald et al., 2018; Melero et al., 2020). In addition to a species' own active dispersal, humans can facilitate their movement into and within a region (Di Castri, 1989). This facilitation can occur from intentional or accidental transportations of individuals, or materials that harbor individuals (Kaňuch et al., 2013; Lanner et al., 2021). Complicating the picture of establishment and spread, is that founding individuals may enter regions multiple times from different sources and at a number of locations, before successful colonization occurs (Di Castri, 1989). Thus, to fully understand the ecology of an invasive species colonization and spread we need to know where the founders originated from (i.e., their genetic origin), where and when they were introduced, and how they spread from the introduction sites through the landscape.

It is generally hypothesized that admixture of different genetic lineages from multiple introductions is beneficial to invasive species thanks to adaptive variation and heterozygosity-fitness correlations, although it remains unclear whether admixture has a causal role in population expansion (Rius and Darling, 2014; Dlugosch et al., 2015). However, genetic interactions between isolated populations selected for locally adapted genotypes, may become unfavorable with genetic distance of different lineages. This may be particularly true in later generations due to outbreeding depression and hybrid breakdown—the poor performance of certain hybrids that leads to extinction (Brideau et al., 2006; Novicic et al., 2011). Most often, it is defined as a reduction in fitness below the midparent but studies are too few to have converged on a standard definition of outbreeding depression (see Edmands, 2007). This explains the low representation of admixture in introductions with high levels of source divergence (Ordóñez et al., 2013; Dlugosch et al., 2015), and it is difficult to examine whether admixed populations are more likely to become successful as colonizers than unmixed ones (Rius and Darling, 2014). One way to study dispersal and colonization pattern is to measure the level of gene flow between populations using neutral molecular markers (Parker et al., 1998). If a species disperses primarily over short distances and in a stepping-stone manner, the genetic structure is expected to follow an isolation-by-distance pattern (Kimura and Weiss, 1964). On the contrary, if there is no significant relationship between genetic and geographic distances a species likely disperses with no or few barriers in the landscape. Also, if dispersal is mediated via a vector, it is expected to be reflected in the genetic patterns across populations.

The Roesel's bush-cricket, *Roeseliana roeselii* (Hagenbach, 1822) (Orthoptera: Tettigoniidae, synonym: *Metrioptera roeselii*) is a small (12–18 mm) bush-cricket common in central and eastern Europe (Bellmann, 2006). It is currently expanding its range in Sweden and other northern European countries (Poniatowski et al., 2012; Eriksson et al., 2013; Preuss et al., 2014, 2015; Beckmann et al., 2015). Passive dispersal of individuals by human transportation of grass-stems (hay) used for egg deposition may facilitate the colonization of distant habitat patches (De Jong and Kindvall, 1991; Wagner, 2004; Kaňuch et al., 2013), and consequently affect the spatial population genetic pattern. In the time of this study, the species distribution in central Sweden predominantly extended across an area of approximately 120 × 140 km in the Lake Mälaren region.[1] The core area of this isolated population has the highest local genetic diversity and its location suggest that *R. roeselii* have been introduced via sea cargo to the banks of the westernmost bay of lake Mälaren (De Jong and Kindvall, 1991; Preuss et al., 2015). This region, with a historical homestead established by the Swedish king Gustav Vasa and his descendants in the sixteenth and seventeenth century, have well documented and long-running extensive horse and cattle imports where *R. roeseli* could have entered in with cargo (Bäckström, 1924; Montelius, 1993). A royal stud farm and military riding school at the town of Strömsholm in the area has previously been identified as a potential introduction site (Preuss et al., 2015). The nearby grasslands at Kungsör are also potential introduction sites, as large farms in the area have been active for very long time periods (Strengbom, 2019). In line with these theories, molecular analyses have suggested multiple introductions of the species and that founding individuals originate from different regions, most likely from the harbors in the Gulf of Finland or from the southern Baltic coast (Kaňuch et al., 2013).

Detailed studies on the species' ecology (e.g., Ingrisch, 1984; Poniatowski and Fartmann, 2005; Holzhauer et al., 2006; Berggren, 2009), movement behavior (Berggren et al., 2002; Berggren, 2004, 2005; Poniatowski and Fartmann, 2011) and population genetics (Kaňuch et al., 2014, 2021) have increased the understanding of how *R. roeselii* responds to environmental factors during the colonization process and how it successfully colonizes uninhabited areas even with very small propagule sizes. As an omnivorous generalist, that preferentially colonizes tall grassland habitats in agricultural landscapes, it is found in various meadows, leys, grassy field margins around crop fields, ditches, and road verges (Marshall and Haes, 1988; Berggren et al., 2001; Preuss et al., 2011). Forests and intensively grazed pastures are considered to be unsuitable habitats (De Jong and Kindvall, 1991; Ingrisch and Köhler, 1998; Berggren, 2004), and large water bodies are expected to be strong barriers for gene

[1] https://www.artportalen.se/

flow for this mostly flightless species (98–99% of the population; Vickery, 1965; Wissmann et al., 2009). The minority, long-winged individuals, is capable to disperse over longer distances (Hochkirch and Damerau, 2009; Poniatowski and Fartmann, 2011), and thus may play a significant role for local genetic variation (Kaňuch et al., 2021).

Existing knowledge of the likely initial introduction area of the species (Preuss et al., 2015), and that those introductions have occurred from at least two different but adjacent regions within the continuous species range (Kaňuch et al., 2013), offer a very interesting opportunity to further explore ecological aspects of introduced species' colonization and spread. In this study, we particularly aimed to move one step further in understanding the spatial genetic patterns associated with successful colonization. We examined how colonization history and landscape structure affect the spread of the species and its population genetic structure, as a consequence of multiple introductions. To do this we used a set of neutral genetic markers to assign individuals in the study area to their potential founders from the species main range and estimated the levels of admixture across different sites in a fragmented landscape (microsatellite data published previously by Preuss et al., 2015 were thus reused and reanalyzed). We tested three hypotheses: (i) Genetic lineages originating from different sources show an admixed pattern in areas where they meet. (ii) Pair-wise genetic differentiation between populations will be positively correlated with the least cost path distance, if dispersal is limited to movement through suitable habitat and different lineages are not admixed; but (iii) the decrease of genetic diversity from central toward marginal populations will be more pronounced in a lineage that colonize areas with less suitable habitats, if species disperses naturally without significant effect of human-mediated transport.

MATERIALS AND METHODS

Samples

During July and August 2010, we sampled 27–30 short-winged adult individuals of *R. roeselii* from 29 locations in the Lake Mälaren region (**Figure 1**). Altogether 837 individuals were genotyped using a set of eight microsatellite markers developed for this species (MR2-42, 3-24, 3-34, Holzhauer and Wolff, 2005; Metroe08, 16, 19, 24, 27, Kaňuch et al., 2010). These are the same eight markers that were used in Preuss et al. (2015). All details on specimens' collection, DNA extraction from muscle tissue, multiplex PCR protocols with fluorescently labeled primers, conditions for reactions and scoring of alleles are described in Preuss et al. (2015). Therein are reported also basic population-genetics characteristics, including sample size, allelic richness, unique alleles, heterozygosity, fixation index, and results of Hardy-Weinberg tests for each sampling site. All samples were in Hardy-Weinberg equilibrium and the pairs of microsatellites did not exhibit significant linkage disequilibrium. Three loci (Metroe19, MR2-42, and MR3-24) exhibited some elevated frequency of null alleles (20–25%) across all locations when tested using the Chakraborty et al.'s (1994) and Brookfield's (1996) methods in the package "PopGenReport" 3.0.4 (Gruber and Adamack, 2019) of the R 3.6.3 software (R Core Team, 2020). Aware of possible bias that might result from this effect we kept these markers for further analyses to not reduce available dataset and to lower resolution of determined genetic structure.

Genetic Structure and Differentiation

To obtain a robust support for identification of genetically homogeneous clusters of individuals in our samples we applied three different approaches. Firstly, we used an individual based clustering method implemented in the software Structure 2.3.4 (Pritchard et al., 2000; Hubisz et al., 2009). We ran the admixture model with correlated allele frequencies without the prior population information and degree of admixture $\alpha = 1$. For each value of K (range 1–29), we conducted 20 independent runs with uniform priors using a burn-in of 100,000 iterations followed by 100,000 Markov chain Monte Carlo iterations. We discarded all individuals with > 20% missing genotypes (i.e., six individuals) and there were no identical multilocus genotypes present in the dataset. The number of genetic clusters K in the data set was inferred by the ΔK method (Evanno et al., 2005), which finds the breakpoint in the slope of the likelihood distribution for different K values, using the Structure Harvester Web 0.6.94 (Earl and von Holdt, 2012), and also through Q-matrix correlations, which identified the stable K solutions (identify anomalous runs), implemented in the R package "CorrSieve" 1.6–8 (Campana et al., 2011). Outputs of the Structure analysis were visualized with the Clumpak program (Kopelman et al., 2015). Secondly, to identify possibly weak spatial genetic patterns, we analyzed spatial autocorrelation in the genetic data using MEMGENE analysis by the R package "memgene" 1.0.1 (Galpern et al., 2014). This approach uses a regression framework which visualizes only statistically significant spatial patterns. Predictors are generated using Moran's eigenvectors maps (MEM) from sampled locations (pairwise Euclidean distances among individuals) and the response variables are individual genetic distances (proportion of shared alleles, D_{PS}). Thirdly, we calculated pairwise estimates of genetic distances among sampled locations and between determined genetic clusters using D_{PS} (Bowcock et al., 1994) and G'_{ST} (Hedrick, 2005), thus an individual- and a population-based estimator, respectively. These two different measures of genetic distance were explored using heatmaps and dendrograms of hierarchical clustering in the R package "adegenet" 2.1.3 (Jombart, 2008).

Founder Assignment

The assignment of samples collected in the Lake Mälaren region to potential founder populations was performed using a machine-learning framework implemented in the R package "assignPOP" 1.2.0 (Chen et al., 2018). A naïve Bayes classification method (a simple probabilistic classifier with strong independence assumptions between the features) was used as a default setting of this package to build predictive model which estimated individual membership probabilities in the study area using baseline microsatellite data that represented two distinct genetic lineages

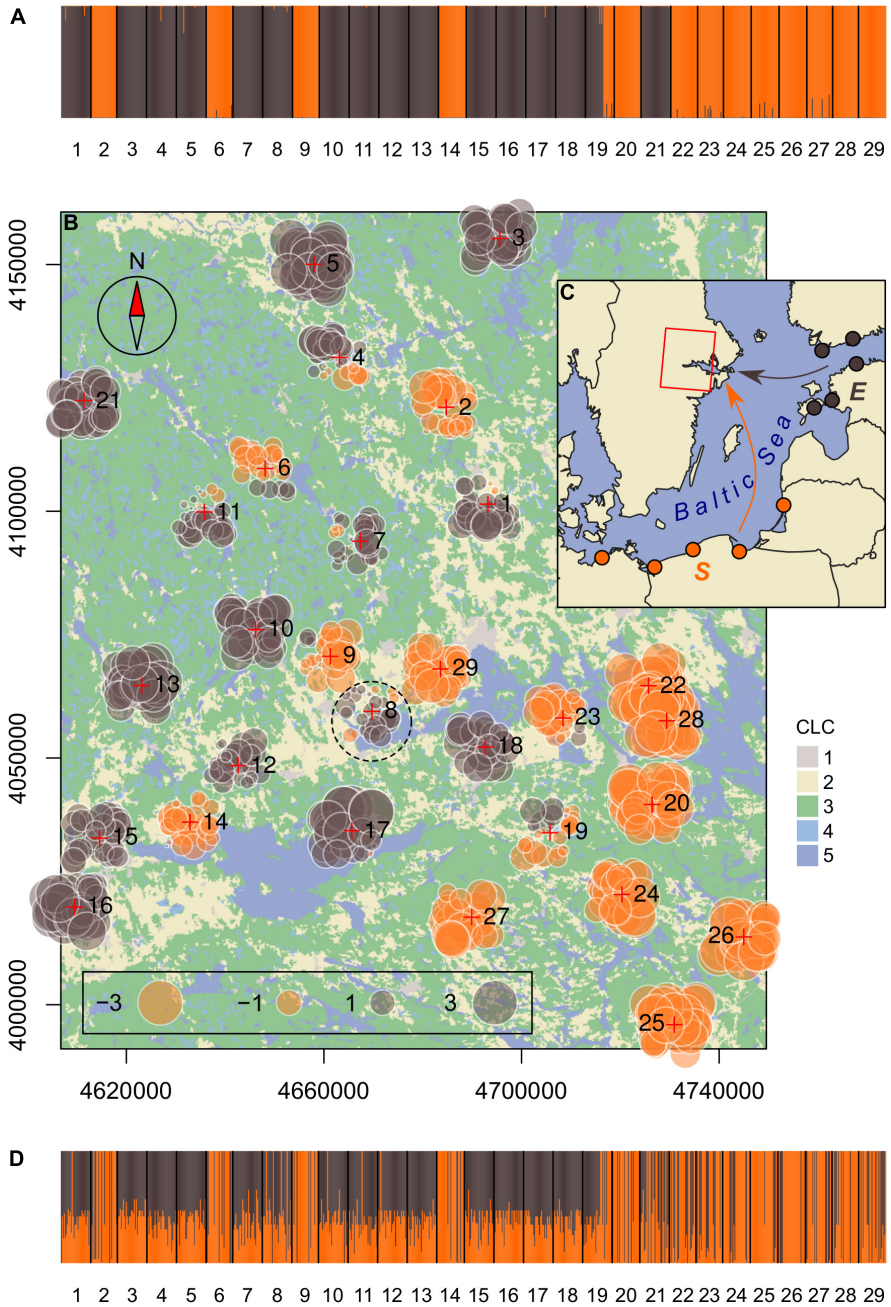

FIGURE 1 | Map of the study area with locations of the 29 sampling sites of *Roeseliana roeselii* (crosses) in the Lake Mälaren region in central Sweden. The main land-cover classes categorized by the Corine Land Cover inventory (1, artificial surfaces; 2, agricultural areas; 3, forest and seminatural areas; 4, wetlands; 5, water bodies) and suggested area of introduction (dashed circle) are depicted. The coordinate reference system is ETRS89/LAEA Europe (meters). **(A)** Genetic structure of *R. roeselii* samples in the study area as inferred by the Structure admixture analysis. **(B)** Spatial MEMGENE analysis of the samples (MEM1 axis). Individuals with similar MEM scores (circles of similar size and color) suggest spatially homogenous genetic clusters. **(C)** Potential source populations (full circles) represent two distinct genetic lineages (*E*, eastern; *S*, southern) and are most likely co-founders of the populations in the study area (Kaňuch et al., 2013). **(D)** Membership probability plot from the assignment test. Individuals in the stacked bar plots are represented by vertical bars divided into parts proportional to their proposed ancestry in determined genetic clusters or membership to source population, respectively.

along the Baltic coast and likely co-founders of populations in central Sweden. Thus, five samples (120 individuals) from Finland and Estonia are hereafter called the "eastern" lineage, while five other samples (120 individuals) from Lithuania, Poland and Germany represent the "southern" lineage (Kaňuch et al., 2013). Alleles of four loci (Metroe07, Metroe08, Metroe19, and Metroe27) sized in both datasets were available for this assignment test.

Landscape Genetics

Information on landscape composition was extracted from the Corine Land Cover data (100 m GeoTiff raster, CLC 2018 version 20).[2] We classed the land-cover categories according to the assumed cost of dispersal that individuals experience when moving through different types of habitats (Sawyer et al., 2011). Based on previous studies on the species presence in the landscape (Preuss et al., 2011), agricultural areas were expected to be positively correlated with presence of the species (i.e., least costly for the species to move through, weight = 1). To other habitats more dispersal cost was attributed: weight = 2 for artificial surfaces as rural settlements and road networks, weight = 3 for wetlands as marshes and peat bogs. Forests and seminatural areas were considered unsuitable habitat (weight = 5), and lakes and waterways were classed as being most costly to move across (weight = 10). Using of Least-Cost Path plugin of the QGIS 3.8.1 software[3] we created a cost surface map of the classified land-cover categories and calculated least cost path distances between all sampled sites (**Supplementary Figure 1**). Besides the least cost path distance, we measured also Euclidean distance (the geographic distance between sites without additional effects of landscape elements on gene flow). The isolation-by-distance (IBD) pattern in sampled populations was tested using Mantel test between matrices of genetic and both geographic distances in the R package "adegenet." For genetic matrix we used chord distance D_C (Cavalli-Sforza and Edwards, 1967).

Finally, to test the central-marginal hypothesis we employed a generalized additive model (GAM) for geospatial interpolation of the genetic diversity of *R. roeselii* in the study area. Using the previous knowledge about correlations between different estimates of genetic diversity (Preuss et al., 2015), we selected mean allelic richness per locus and sampling site as a suitable representative of genetic diversity. Smooth functions of predictor variables (x, y coordinates of sampling sites) were estimated and the model was visualized using the R packages "mgcv" 1.8-28 (Wood, 2019) and "raster" 3.0–12 (Hijmans, 2020). To test whether the proportion of land-cover classes differed between the areas colonized by different genetic introduction lineages, we fitted a model of independence for two-way tables that was visualized in mosaic plot using the R package "vcd" 1.4–6 (Meyer et al., 2020).

RESULTS

In the outputs of the admixture model simulated in the Structure analysis, both methods ΔK and Q-matrix correlations detected stable genetic structure at $K = 2$ (**Figure 1A** and **Supplementary Figures 2, 3**). Interestingly, all sampling sites except one was represented by individuals that belonged to only one of the two genetic clusters. Sampling site number 19 was the only location where individuals of both genetic clusters occurred together. This pattern was seen also in the MEMGENE analysis where the MEM variables indicated higher level of admixture of the two genetic clusters around the area of initial introduction (smaller absolute MEM scores), and higher genetic differentiation toward marginal zones of the current species distribution (greater absolute MEM scores; **Figure 1B**). The proportion of genetic variation along MEM axes ($R^2_{adj} = 0.28$) was sufficient to identify the spatial genetic structure. MEM1 axis explained most, 65%, of the spatial genetic variation (MEM2 and MEM3 explained 7 and 5%, respectively). The genetic structure of samples matched perfectly to the results of the assignment test. Most individuals of one genetic cluster in the lake Mälaren region were assigned to the southern genetic lineage and the second cluster appears to have been established from founders of the eastern lineage (**Figures 1C,D**). Contrary to the southern lineage, eastern lineage individuals in stacked barplots were assigned with a lower 70% membership probability which appears to result from a more limited set of available microsatellite loci which did not allow for better resolution in this analysis (see section "Materials and Methods"). Possibly the same technical restraint (low number of alleles that were identical between baseline and test data) assigned a number of individuals of the southern (orange) genetic cluster to eastern (brown) founder lineage.

Genetic differentiation of the inferred genetic clusters was very high (mean $\pm$ *SD*; $D_{PS} = 0.624 \pm 0.055$, $G'_{ST} = 0.605 \pm 0.079$) suggesting no or very little gene flow between the main clusters and two different estimators of genetic distance revealed consistent pattern (**Figure 2**). Therefore, testing of spatial correlations between matrices of genetic and geographic distances was meaningful only within each genetic lineage. Individuals from sampling site 19 were excluded from further spatial analyses as a consequence of the significant proportion of both genetic lineages. The estimated least cost path distances, representing the optimal dispersal routes between populations, were on average 38 and 29% longer than the Euclidean distance in the eastern and the southern lineage, respectively. In contrast to the eastern genetic lineage, neither using Euclidean distance nor least cost path distance resulted in a significant IBD pattern for the local populations of the southern lineage (**Figure 3** and **Supplementary Figure 4**). Differences in the IBD pattern were similar to the modeled spatial patterns of genetic diversity in these two lineages. The decrease of genetic diversity from the introduction sites toward the marginal areas was more pronounced in the eastern lineage situated in more forest dominated landscapes, than in the southern lineage situated in landscapes dominated by arable land (**Figure 4**).

DISCUSSION

We found a striking spatial genetic pattern consisting of two lineages which originate from two parapatric founding populations that today coexist in a large and naturalized population of the Roesel's bush-cricket outside the native species range. Despite that gene flow creates a stepping stone like pattern of genetic distances among local populations, and that there is a decrease of genetic diversity from central toward marginal areas, there was almost no gene flow between these lineages. Some kind

[2]https://land.copernicus.eu/

[3]https://qgis.org/

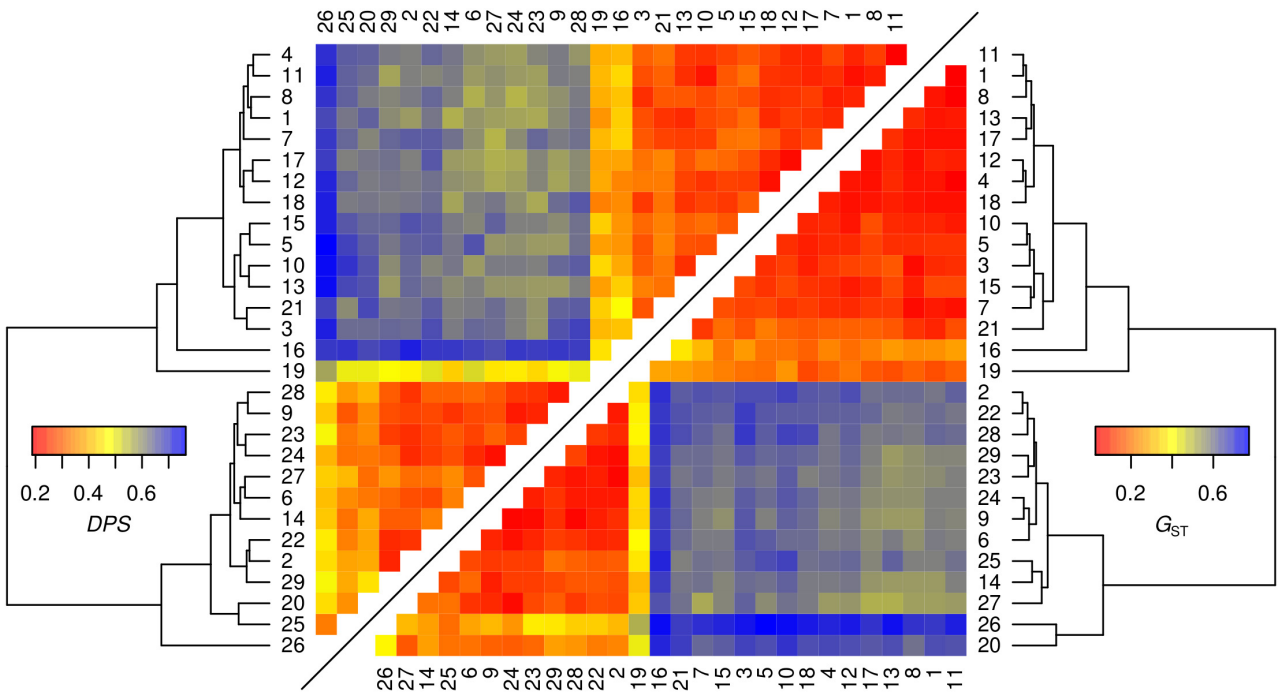

FIGURE 2 | Pairwise heatmaps of genetic distances between the 29 sampled sites with hierarchical clustering dendrograms calculated by two different estimators (proportion of shared alleles D_{PS} and Hedrick's G'_{ST}) based on genotypes determined on eight microsatellites loci.

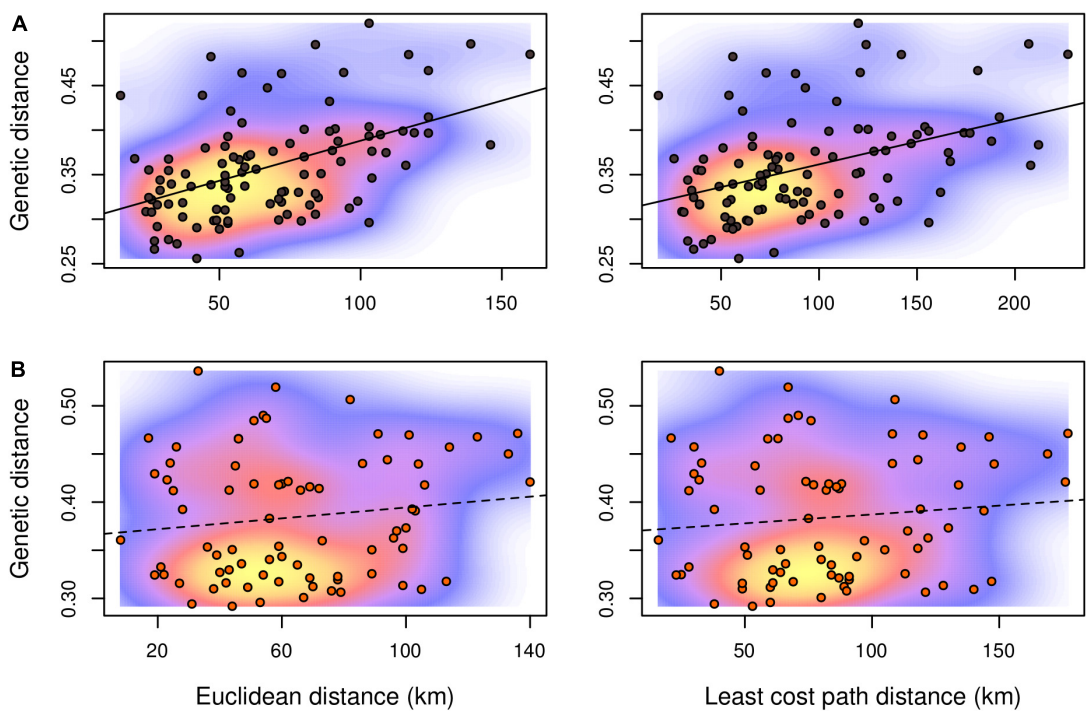

FIGURE 3 | Isolation-by-distance scatterplots with kernel density estimations for pairwise values between *R. roeselii* local populations sampled in the Lake Mälaren region. **(A)** Samples assigned to the eastern and **(B)** to the southern genetic lineage, respectively. Mantel correlations are indicated by full (significant, $p < 0.05$) or dashed (non-significant, $p > 0.05$) lines.

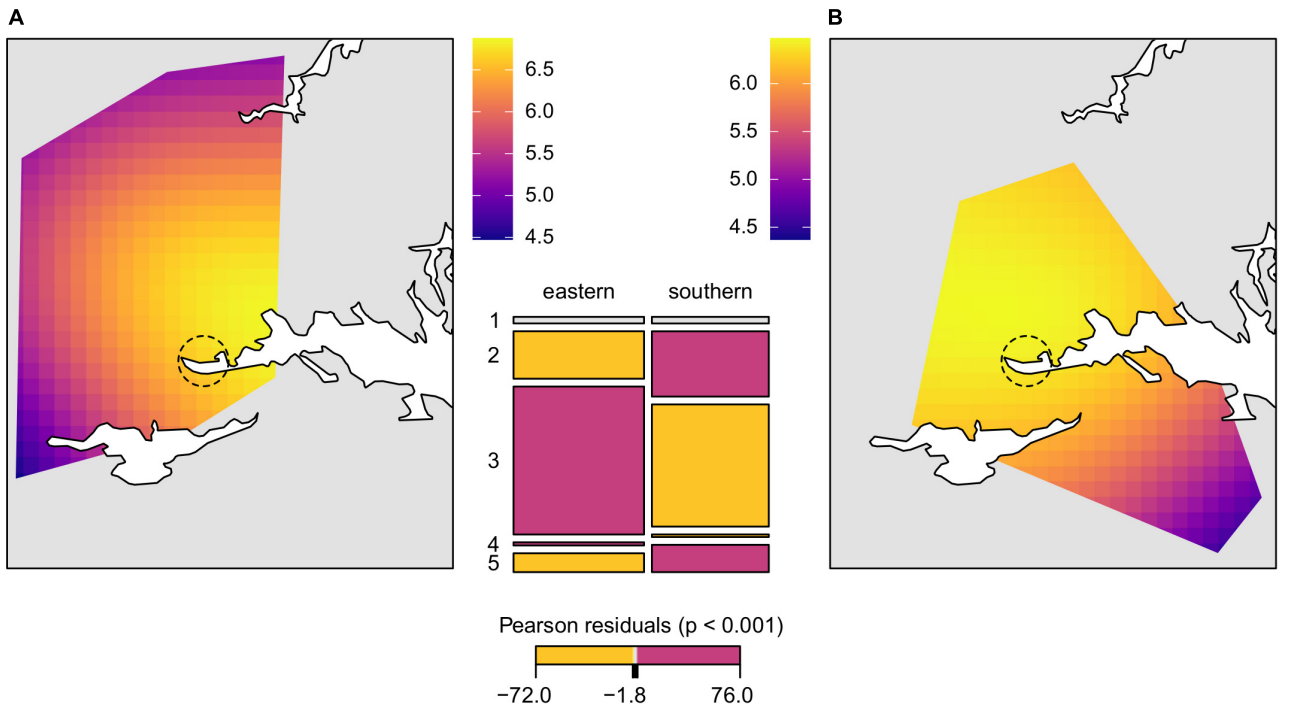

FIGURE 4 | Geospatial interpolation surfaces fitted to the GAM model of allelic richness (colored raster polygons) in **(A)** the eastern and **(B)** the southern genetic lineage with superimposed large water bodies in the study area (white). Dashed circle marks suggested area of introduction. Mosaic plot (mid figure) presents the proportion of the main Corine Land Cover classes (1, artificial surfaces; 2, agricultural areas; 3, forest and seminatural areas; 4, wetlands; 5, water bodies) in the areas (minimum convex polygons) colonized by the different lineages. Each tile is colored to show the deviation from the expected frequency (residuals) from a Pearson χ^2-test (red—significantly more, yellow—significantly less than expected, gray—non-significant).

of mechanism, which is not due to physical distance, appears to exist that keeps genetic lineages separated. We have earlier shown that the colonization of *R. roeselii* in central Sweden is a result of more than one introduction event (Kaňuch et al., 2013). The fact that lineages have continued to stay separated truly was a surprise, especially considering the fact that the species has had a very long time to admix. The two lineages were introduced from the Baltic coast independently and we expect that propagules from the eastern genetic lineage (Gulf of Finland) were introduced more recently, maybe 5–10 decades ago since the species range is still progressing northwards in the source area (Karjalainen, 2009). While it is likely that in the southern lineage populations were established before the nineteenth century from the former Kingdom of Prussia (nowadays Poland and Germany). The current and isolated range of both lineages is similar, but they thrive genetically unmixed. This in spite of that they have been spatially more or less mixed around the Lake Mälaren for many dozens of generations. This finding is in strong contrast to the hypothesis that different genetic lineages will admix when introduced to the same area.

One possible mechanism behind this pattern can be that the lineages (**Figure 2**) were introduced at sites with some distance between them (e.g., terrestrial distance between potential introduction sites Strömsholm and Kungsör is 25 km) and that they, in combination with two different genetic setups from the start, adapted independently to the local conditions (Ma et al., 2020; see also Cassel-Lundhagen et al., 2011; Kaňuch et al., 2020) before colonizing the larger area. The diversified original gene pool and local adaptation hypothesis would explain the observed pattern if the admixture of alleles resulted in loss of locally adapted genotypes, and a hybrid offspring less viable than the respective ancestral genotypes (e.g., Brideau et al., 2006; Novicic et al., 2011; Rius and Darling, 2014). Rapid evolution of genotypes adapted to local conditions accords well with the fact that there is no evidence that populations of this species suffer from recent bottlenecks and/or high inbreeding level (Kaňuch et al., 2014). Thus, one could expect that there is a substantial genetic capacity to adapt to new environments and little effect of isolation on heterozygosity-fitness correlations. This hypothesis could be further tested with controlled mating experiments. What this finding also raises, is a potentially negative impact that such adaptive process could have for conservation introductions. Conservation management focused on increasing population sizes and species' distributions by the addition of new individuals, could be less successful if existing adaptions are already present in the target species.

An alternative mechanism that would produce this genetic pattern could be the presence of a post-mating or post-zygotic reproductive barrier and hybrid breakdown phenomenon. It can be caused on one hand by mito-nuclear incompatibilities lowering the fitness of hybrids carrying different lineages' mitochondrial haplotypes and nuclear genotypes, what has been

seen also in related insect species (e.g., Marchant, 1988; Morgan-Richards and Wallis, 2003). On the other hand, *Wolbachia* bacterial infection manipulates the physiology and reproduction of its hosts and can induce cytoplasmic incompatibility. For example, if uninfected females of one lineage mate with infected males of the other lineage, hybrid offspring or hybrid F2 males can suffer increased mortality (Vala et al., 2000; Bordenstein et al., 2001). Because the frequency of *Wolbachia* infection is lower toward higher latitudes (Ahmed et al., 2015), this mechanism has an increased likelihood to exist in situations where lineages originate from latitudinally different regions, as in this study (**Figure 1C**). Due to the lack of biological material from specimens that were used in our study, these hypotheses could not be tested.

To a large extent the least cost pathway analysis did reflect what is known about the species' movement behavior and its dispersal pattern in previous landscape studies (Berggren et al., 2001, 2002). Even though the dispersal of short-winged forms is tightly linked to movement through suitable habitat and linear elements, this may not be the same for individuals that are accidentally transported by humans. Human-aided dispersal may considerably affect the genetic structure of a population (Hochkirch and Damerau, 2009), similar to the effect of long-winged individuals. Several studies have found that least cost pathways can be poor in estimating the dispersal of individuals that have a different type of dispersal behavior (Simmons and Thomas, 2004; Poniatowski and Fartmann, 2011). Due to the very low proportion of long-winged individuals in the populations (own data) we assume that besides that landscape characteristics predict the species' occurrence (Preuss et al., 2011), the high frequency of human transportation of agricultural goods and animals among local farms play an important role for the overall spatial genetic pattern of the Roesel's bush-cricket population in the study area. From the genetic pattern seen in the southern lineage, these local populations may be more affected by this mechanism as neither Euclidean nor least cost path distance resulted in a significant IBD pattern (**Figure 3B**). This also makes it clear that if reproductively separated genetic clusters are combined in an IBD analysis, this can produce fallacious pattern due to that genetic distances are calculated also for pairwise combinations without possible gene flow (see **Figure 3** in Preuss et al., 2015).

To understand the role of humans' actions in facilitating species spread through the landscape, detailed knowledge not only about the species' ecology but also the opportunities offered by land managers is needed. To be able to analyze the human-invasive species interactions in more detail, comprehensive data of detailed land use management activities and a knowledge of how these relate to opportunities of spread (e.g., by mediation of transport) are required. Human aided colonization and spread of species often go unnoticed when they happen (Hammer and Jensen, 2019; Sherpa et al., 2020). This is partly due to a lack of awareness on how one's actions link to likelihood of invasions (Shannon et al., 2019, 2020). With an increasing trade of agricultural goods and organisms both within and between countries, people actively managing the land such as farmers may increasingly act as facilitators of invasive species spread. This will not always directly affect the farmers themselves when it comes to some organisms (which primarily constitute a threat to natural communities), but for other organisms, this may be a direct threat to domestic species important to these land managers (Bajwa et al., 2019; Pardo et al., 2020).

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

AC-L and ÅB conceived the project. SP collected and genotyped the samples. PK analyzed the data and prepared the figures. PK, ÅB, and AC-L wrote the manuscript. SP and GN reviewed drafts of the manuscript. All authors approved the final draft.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.812079/full#supplementary-material

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