RESEARCH ARTICLE

Spatial structure and dispersal dynamics in a house sparrow metapopulation

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Abstract

1. The effects of spatial structure on metapopulation dynamics depend upon the interaction between local population dynamics and dispersal, and how this relationship is affected by the geographical isolation and spatial heterogeneity in habitat characteristics.

2. Our aim is to examine how emigration and immigration of house sparrows *Passer domesticus* in a Norwegian archipelagic metapopulation are affected by key factors predicted by classic metapopulation models to affect dispersal—spatial and temporal variation in population size, inter-island distance, local demography and habitat characteristics.

3. This metapopulation can be divided into two major habitat types: (a) islands closer to the mainland where sparrows breed in colonies on farms, and (b) islands without farms, situated farther away from the mainland where sparrows are exposed to harsher environmental conditions.

4. Dispersal was spatially structured within the metapopulation; there was proportionally and numerically less emigration and immigration involving farm islands, as compared to non-farm islands. Furthermore, emigration and immigration occurred mostly between nearby islands. Moreover, emigration in response to spatial differences in mean population size differed between the habitat types, but populations with large mean received more immigrants in both habitat types. The number of emigrants and immigrants was negatively related to long-term recruit production, which was not the case in non-farm islands. The proportion and number of emigrants was positively related to temporal increases in recruit production on farm islands, however not on non-farm islands.

5. Our results demonstrate that spatial heterogeneity in environmental conditions influences how spatial variation in long-term mean population size, and temporal and spatial variation in recruit production, affects dispersal dynamics. The spatial structure of this metapopulation is therefore best described by a spatially explicit

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model in which the exchange of individuals within each habitat type is strongly affected by the degree of geographical isolation, population size and recruit production. However, these relationships differed between the two habitat types; non-farm islands showing similarities to a mainland-island model type of structure, whereas farm islands showed features more associated with source–sink or balanced dispersal models. Such differential dispersal dynamics between habitat types are expected to have important consequences for the ecological and evolutionary dynamics within this metapopulation.

KEYWORDS

density dependence, eco-evolutionary feedback, emigration, habitat quality, immigration, population dynamics, population size, recruit production

1 | INTRODUCTION

Dispersal has profound consequences for the evolutionary and ecological dynamics of spatially structured populations (Benton & Bowler, 2012; Garant et al., 2005; Hanski, 1999; Lande et al., 1998; Postma & van Noordwijk, 2005; Sæther, Engen, et al., 1999; Stacey & Taper, 1992). The exchange of individuals influences the rate of local adaptation (Debarre et al., 2013; Engen & Sæther, 2016; Gandon et al., 1996; Hadfield, 2016; Lenormand, 2002; Ronce, 2007; Ronce & Clobert, 2012), the strength of selection (Rousset, 2012), the genetic structure of a metapopulation (Coulon et al., 2012; Reid & Arcese, 2020) and the risk of local extinctions (Brown & Kodric-Brown, 1977; Stacey & Taper, 1992). Dispersal may also reduce the strength of density dependence (Engen et al., 2002), increase population densities (Ives et al., 2004) and increase spatial synchrony in local population fluctuations (Lande et al., 1999). Furthermore, temporal variation in population sizes has also been shown to affect dispersal rates within metapopulations (Travis et al., 1999). This generates a feedback between population size and dispersal rates that links the ecological causes of dispersal with its consequences for population dynamics, at both short- and long-term time-scales (Sæther, Engen, et al., 1999).

A general theoretical framework for studying the effects of spatial structure on population dynamics was provided by MacArthur and Wilson (1967) and Levins (1969). Their models constitute two extremes of a continuum related to the effect patch size variation on colonization and extinction (Hanski & Gyllenberg, 1993). At one end of this framework for analysing the dynamical consequences of spatial structure is a model of a 'mainland' population that never goes extinct and affects the population dynamics in other patches (MacArthur & Wilson, 1967). At the other end is a model where all subpopulations are equal and are characterized only by their occupancy (Levins, 1969), although even this simplified model provides several important non-intuitive insights, for example that a metapopulation can only persist if each local population establishes at least one new population during its lifetime (Hanski & Gilpin, 1997). Furthermore, these models predict that increased patch occupancy is favoured by increasing patch size and shorter inter-patch distances, and that this effect is based solely upon the ratio between colonization versus extinction rates and not upon local dynamics (Hanski, 1999; Hanski & Gilpin, 1997; Tilman & Kareiva, 1997). An important extension of Levins' (1969) approach was suggested by Hanski (1994) and was based upon analyses of incidence functions. This approach made it possible to quantify the effects of spatial location and patch quality on the probability of extinction and colonization, allowing quantitative exploration of the influence of spatial heterogeneity on metapopulation dynamics (Hanski, 1999; Hanski & Ovaskainen, 2000).

Another important advance in the application of spatially structured models was provided by Pulliam (1988, 1996) and Pulliam and Danielson (1991), who introduced local dynamics into metapopulation models. In source–sink models, individuals disperse from local patches with high population growth rates (sources) to patches with growth rates lower than one (sinks) that would go extinct without immigration. Importantly, such permanent differences among patches tend to make metapopulation viability strongly dependent upon specific source populations (see Holt & Gomulkiewicz, 1997; Kawecki, 2004, for overviews).

These spatially structured models assume a stable environment and that dispersal is a fixed function of local population size. However, annual fluctuations in environmental conditions may cause temporal variation in population sizes, which in turn may affect emigration or immigration rates (see e.g. Pärn & Sæther, 2012). If dispersal is driven by common environmental variation affecting population dynamics over large areas, this can lead to the mainland-island type of spatial structure in which colonization of local patches occurs from a large common pool of individuals (Lande et al., 1998). Furthermore, in general, emigration is assumed to increase and immigration to decrease with increasing population size, due to greater resource competition and/or stronger social interference effects (Clobert et al., 2001). However, it is also hypothesized that if larger population sizes or greater recruit production reflect favourable environmental conditions, then this may reduce emigration rates and attract more immigrants (Doligez et al., 2002; Enfjäll & Leimar, 2009;

Fernández-Chacón et al., 2013; Ray et al., 1991; Serrano & Tella, 2003; Stamps, 1988). Importantly, such differences in the patterns of density-dependent dispersal will strongly affect metapopulation persistence (Sæther, Engen, et al., 1999).

Understanding dispersal dynamics in the light of spatially explicit metapopulation models, as suggested by Harrison (1991), represents a key element for predicting responses to environmental change and assessment of extinction risks. This requires knowledge of how permanent differences in patch characteristics are distributed in space, detailed knowledge about the inter-patch movement of individuals and how dispersal depends upon isolation, and local population size fluctuations (Dallas et al., 2021; Hanski, 1999). Such data are extremely difficult to obtain under natural conditions, because it requires a large proportion of individuals to be individually marked within a geographical area and that the study locality is large relative to dispersal distances (Millon et al., 2019). An integrated approach is therefore needed, which combines the analyses of temporal local population dynamics and spatial differences in the ecological and demographic characteristics of populations with detailed data on inter-population movement patterns (Table 1).

In this study, we examine inter-island dispersal dynamics in a metapopulation of house sparrow *Passer domesticus* in northern Norway, which has been monitored since 1993. This long-term study provides a major opportunity to examine the effects of spatial and temporal variation in population characteristics on emigration and immigration in a free-living vertebrate. Previous investigations into this metapopulation have suggested a negative density-dependent effect on immigration rate (Tufto et al., 2005), and a positive effect of population density on emigration rates in some islands (Pärn et al., 2012). In the present study, we aim to characterize the patterns of emigration and immigration in this metapopulation and relate those to key dispersal characteristics of classical metapopulation models (Table 1).

2 | MATERIALS AND METHODS

2.1 | Study populations

House sparrow data from a 22-year period (1993–2014) were obtained from 11 island populations in an archipelago off the coast of Helgeland in northern Norway (66.30°–66.80°N, 12.00°–13.10°E; Figure 1). The 11 study islands are surrounded by many smaller, uninhabited islands currently without any house sparrow populations, and are part of the metapopulation and have hosted sparrow populations for much of the period between 1993 and 2014 (Baalsrud et al., 2014). In addition, there are a few small sparrow populations along the mainland coast, but from the size of these populations they are unlikely to be contributing much at all in exchange with the insular metapopulation under study. House sparrows have been present on all study islands throughout most of the study period (Baalsrud et al., 2014). On three islands, surveys were initiated in 1994 (Lovund, Lurøy-Onøy and Sleneset), and one population was established by a

natural colonisation event in 1998 (Aldra). The islands can be divided into two different habitat types, based upon the presence of farms ('farm islands' vs. 'non-farm islands') and distance from the mainland. The farm islands (Aldra, Gjerøy, Hestmannøy, Indre Kvarøy, Lurøy-Onøy and Nesøy; Figure 1) are located closer to the mainland, and house sparrows breed mainly in and around dairy farm buildings. On these islands, house sparrows obtain most of their food around and inside the farms (e.g. animal feed) and have access to shelter in barns during winter. Birds in the farm populations may thus experience more benign environmental conditions with more stable food sources. Conversely, the non-farm islands (Lovund, Myken, Selvær, Sleneset and Træna; Figure 1) are located further out in the sea farther away from the mainland. On these islands, house sparrows do not have easy access to shelter, and food is irregularly supplied at garden bird feeders by local people. The more unpredictable food sources and exposure to harsher conditions on the non-farm islands may result in lower survival rates. Accordingly, there is large spatial variation in population growth rates (Sæther, Ringsby, et al., 1999) and demography (Stubberud et al., 2017) among the populations.

Fieldwork was conducted during the breeding season, from early May until the middle of August. The presence of individuals was determined by monitoring colour-ringed individuals (see below), catching sparrows in mist nets and ringing any unmarked individuals. Each population was thoroughly searched for nests (with the exception of Lurøy-Onøy, and the non-farm islands prior to 1999, for logistical reasons). Most nests are found in barns and cowsheds or in nest boxes. In this area, house sparrows lay between one and three clutches per season (Husby et al., 2006). During incubation and nestling periods, nests were visited two or three times. When nestlings were 7–12 days old, they were individually marked with a unique combination of metal and plastic colour leg rings. In September–October, birds were captured on all islands to mark previously unmarked individuals and to record individuals present in the populations during the period when most natal dispersal occurs (Ranke et al., unpubl results). For further description of field procedures, see Sæther, Ringsby, et al. (1999), Ringsby et al. (2002) and Jensen et al. (2006). The high proportion of marked individuals in the study populations (typically >80%) combined with the high sampling effort allowed close monitoring of the life histories of the majority of individuals. The remaining <20% of the population, that is unmarked individuals, usually consisted of residents, such as fledged juveniles from undetected nests or adult individuals not formerly captured. Note that juveniles captured after summer (i.e. in autumn and later) were not included in the analyses to ensure that all individuals used in the present analyses were confidently assigned to the island on which they hatched. Furthermore, genetic assignment of newly recruited individuals with unknown origin suggests that a large proportion of these birds (*c.* 29%) are in fact immigrants from another island within our island metapopulation study system, and that there are nearly no immigrants from outside this system (Saatoglu et al., 2021).

This study focuses on natal dispersal, which constitutes the majority of inter-island dispersal in this metapopulation (i.e. >99% cases; Altwegg et al., 2000; Pärn et al., 2009, 2012). Because our

TABLE 1 Summary of theoretical models of dispersal in spatially structured populations, their predictions and evidence in support of them from our house sparrow metapopulation

Model	Emigration		Immigration	
	Prediction	Support (yes/no)	Prediction	Support (yes/no)
Levins' metapopulation[a]	Independent of patch size, inter-island distance and local population dynamics	No support (Table 2) Negatively affected by inter-island distance. Dependent on habitat type Mean population size, as a proxy of patch size, had a negative effect on the proportions of emigrants in farm islands, but a positive effect on the non-farm islands	Independent of patch size, inter-island distance and local population dynamics	Mixed support (Table 2) No effect of inter-island distance Dependent on habitat type. More immigration to islands with large mean population size
Mainland-island[b,c]			Long-distance immigration, independent of local dynamics	Equivocal, but only a few individuals were recorded immigrating from the mainland
Source–sink dynamics[d]	Increased emigration from populations with growth >1	Yes, for the farm islands (Table 3) Proportionally and numerically more emigrants in years with higher numbers of recruits per adult on farm islands, but not on non-farm islands	Increased into populations with growth <1	Yes, on farm islands (Table 3) Less immigration into population with long-term large recruit production on farm islands, but not on non-farm islands (see also Table S3)
Balanced dispersal[e,f]	Island-specific emigration rates increases with immigration rates Emigration rates inversely proportional to population size	Yes, see Figure 4 Yes, on farm islands (Table 2) On farm islands, there was proportionally less emigration from populations with large mean population size. However, non-farm islands with larger populations had proportionally more emigration than farm islands	Island-specific immigration rates increase with emigration rates	Yes, see Figure 4
Conspecific attraction[g]	Decreased proportion or numbers of emigrants from populations with large population size	Yes, on farm islands, see Table 2 Proportionally less emigrants from islands with large mean population size. No evidence on non-farm islands, in which larger mean population sizes were associated with numerically more emigration	Increased proportion or numbers of immigrants into populations with large population size	Yes, in both habitats, see Table 2 Numerically more immigration into populations with larger mean population size on farm and non-farm islands (see also Tables S4 and S5)
Conspecific reproduction attraction[h]	Decreased emigration from productive populations	No, see Table 3 Farm islands had proportionally and numerically more emigration when recruit production was above mean, on farm islands. This effect was not present on non-farm islands	Increased immigration into productive populations	No, see Table 3 On farm islands, there was a tendency for proportionally less immigrants into populations with long-term low average number of recruit per adult. There was no such effect in non-farm habitat type. No effects of yearly deviations in recruit production from the long-term mean on immigration in either habitat types

[a]Levins (1969).
[b]MacArthur and Wilson (1967).
[c]See also, Harrison (1991), including habitat quality.
[d]Pulliam (1988, 1996) and Pulliam and Danielson (1991).
[e]McPeek and Holt (1992).
[f]See also, Doncaster et al. (1997).
[g]Stamps (1988).
[h]Doligez et al. (2002).

main interest involved individuals that were potential contributors to local demography and gene flow in the breeding population, only recruits (individuals that were registered in their second calendar year, when most house sparrows start to breed; Anderson, 2006) were included, although non-recruiting dispersers may also affect population dynamics. Proportion emigrants is defined as the number of emigrants, divided by local recruits plus the number of emigrants, and similarly, proportion immigrants is defined as the number of immigrants, divided by local recruits plus the number of immigrants. Individuals that recruited on their natal island were defined as 'local residents'. Individuals that settled on another island than their natal island were recorded as 'emigrants' on their natal island and 'immigrants' on the island of settlement. This implies that emigration represents the combined result of emigration propensity and immigration success. Most dispersers were recorded in their year of recruitment (357 of 376) the year after hatching; with only 19 being recorded in a later year (i.e. using recapture and resighting data from a later year). Furthermore, 'average recruit production' for an island was regarded as all resident recruits plus known emigrants divided by the adult population size. For the non-farm islands, close monitoring of nests started from 2004; thus for the analyses of average recruit production, non-farm islands are not included for the years 1993–2003.

The total study area (c. 1,600 km^2) consists of vast areas of unsuitable habitat (i.e. mostly sea), and it spans many times the range of average house sparrow dispersal distances (90% <36 km; Anderson, 2006; Tufto et al., 2005). Thus, dispersal out of the study area should be minimal, and this allows accurate estimation of emigration and immigration rates for all islands.

Adult population sizes were estimated in a separate model using CMR (capture–mark–recapture; Lebreton et al., 1992) based on data from all ringed adults, to account for differences in recapture probabilities across islands and years (Araya-Ajoy et al., 2021). We adjusted the number of recorded marked adults by dividing it by the island-year-specific resighting rate (Figure 2). Population sizes should therefore be an unbiased underestimate in general, due to the small number of unmarked adult birds in the populations. However, there was some variation in the proportion of unmarked individuals, both among islands and years, which could potentially bias our population estimates. Note also that when resighting rates were below 0.60, the population size estimate was not included in the analysis due to the large uncertainty in the estimate.

In addition, we ran our models assessing the effect of adult population size and average recruit production (Tables 2 and 3) in a CMR framework using RStan (Stan Development Team, 2018), including resighting histories, which enabled us to estimate population sizes and recruitment probability directly in the model. In general, model outputs from these models (Tables S8 and S9) corroborated our findings; however, several relationships showed no or very weak effects due to large credible intervals. The only exception was that these models showed larger immigration rates and numbers into temporally larger and temporally productive populations, in both habitat types (Tables S9 and S10).

There is also substantial annual variation in vital rates (see Ringsby et al., 2002) and population growth rates (see Sæther, Ringsby, et al., 1999) in the local house sparrow populations on these islands, caused by a combination of density dependence and environmental fluctuations. The number of recruits produced per adult was calculated for the five of the farm islands (all except Lurøy-Onøy) where we have sufficient data from the breeding season for the whole period (1993–2014). In the non-farm islands, we included the mean number of recruits produced per adult only for the years 2004–2014.

2.2 │ Statistical analyses

Annual emigration and immigration per island

We examined the factors affecting emigration and immigration to a given island using generalized linear mixed-effect models (see a detailed description in Supporting Information Appendix A1), in which the proportion (binomial) and number (Poisson) of emigrants and immigrants were included as response variables. We used within-subject centring to study the independent effects of temporal versus spatial variation in population size on emigration and immigration (van de Pol & Wright, 2009). Two different measures of population size were thus included as fixed effects: the long-term mean population size for each island (hereafter only 'mean population size') and the annual deviation from the mean population size (hereafter 'deviation from mean population size'). We first scaled population size across all islands by mean centring and dividing by the standard deviation (Table S1). We then estimated the mean population size and measured the deviations from the mean population size for each year. Furthermore, we included habitat type (farm- vs. non-farm islands) as a fixed effect, and the interaction between the population size metric and habitat type to examine habitat-specific population size effects (see Supporting Information for results for each habitat type separately, Tables S4 and S5). Due to the expected negative effect of geographical isolation on dispersal (Tufto et al., 2005), we also included the mean geographic distance to the 10 surrounding study islands to evaluate whether the degree of isolation affected emigration and immigration.

We further evaluated using a separate set of models the effects on dispersal of spatial and temporal variation in the average number of recruits produced per breeding adult. Similarly, as above, we fitted the proportion and number of emigrants and immigrants as response variables and used within-subject centring to tease apart spatial versus temporal effects. We first standardized the number of local recruits produced per adult on the focal island (i.e. resident recruits plus those that emigrated) by mean-centring across all islands and divided by the standard deviation (Table S1). We then estimated the mean for each island and included annual deviations from the mean as a measure of temporal fluctuations in recruit production. By running these models, we could examine an important component of population growth (recruitment rate) separately from models
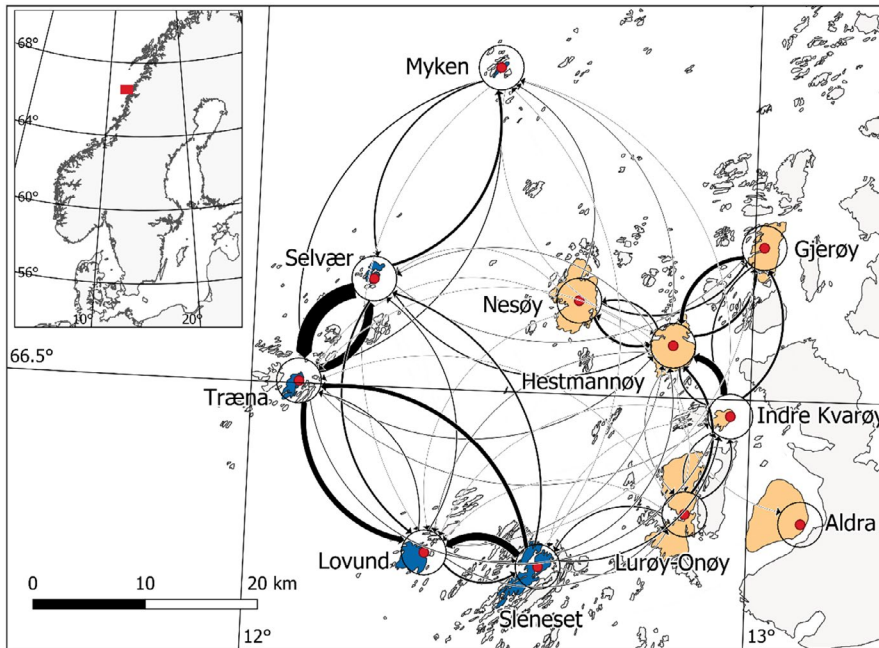
FIGURE 1 Map of the house sparrow metapopulation study area. The islands with names and highlighted with circles are the 11 main study islands used in this study. They are categorized into two different groups based on the presence of farms (six 'farm islands', closest to the mainland, beige fill colour; five 'non-farm islands', blue fill colour). The arrows indicate inter-island dispersal events in the period 1993–2014. The arrow thickness represents the total number of emigrants and immigrants over the whole study period, and the arrow head shows the direction of dispersal
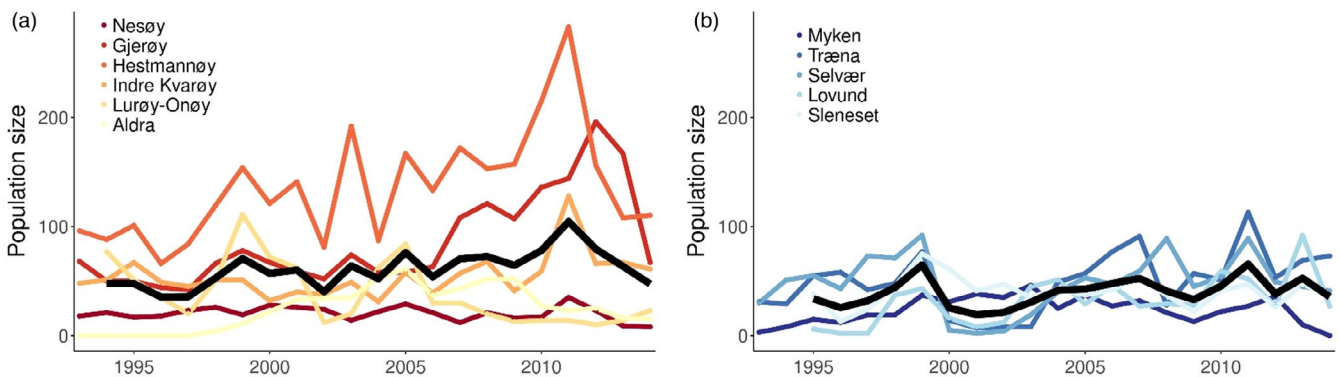
FIGURE 2 Annual population size estimates based on the number of ringed adult house sparrows, adjusted for resighting probability, for farm islands (a) and non-farm islands (b). The solid black line depicts mean for the total metapopulation (note that population size for some islands was not estimated from the start of the study, and therefore total metapopulation size is not reported before 1995, see Section 2)

assessing the effect of population size. In all models, island identity and year were included as random intercepts as well as adding an observation-level random effect (island by year) to account for any overdispersion (Harrison, 2014).

General statistical methods

All analyses were performed using the software *R* version 3.6.2 (R Core Team, 2019). Mixed-effect models were fitted using the GLMMTMB package version 0.2.2.0 (Brooks et al., 2017). We estimated 95% credible intervals (CI) using the 'confint' function, assessing the strength of evidence for an effect based on the degree of overlap of the CIs with zero.

3 | RESULTS

We recorded a total of 2,192 recruits on the 11 main study islands in our house sparrow metapopulation that were ringed as nestlings or juveniles during the summer and recruited to any of the islands the year after. Among those, 376 (17.2%) recruits had dispersed to another island within the metapopulation. Annual adult population sizes (range: 0–283; Figure 2), annual number of local recruits (range: 0–58; Figure S1) and annual number of emigrants (range: 0–14; Figure S2) and immigrants per island (range: 0–21; Figure S3) varied considerably across years and among islands. Consequently, the proportion of emigrants or immigrants among recruits in each population also showed large variation. The average proportion of dispersers among recruits across years and islands was 0.17. On some islands in some years, there

were no immigrants among the new recruits, whereas in other years, all the recruits to the local population were immigrants (see Figure 3).

3.1 | Spatial structure of dispersal

The majority of dispersal events occurred among islands belonging to the same habitat type (n = 227 individuals, non-farm and n = 99 individuals, farm habitat type). Thus, only a few individuals dispersed across habitat types: 19 individuals emigrated from farm islands to non-farm islands, and 31 individuals from non-farm to farm islands (Figure 1; Table S8). There was consistently more emigration and immigration among non-farm islands compared to the farm islands (Tables 2 and 3), and the proportion of recruits that dispersed in the non-farm islands was about twice of that in the farm islands (Figure 4). Independent of habitat type, the exchange of individuals among islands was strongly affected by inter-island distance (Table S8). The distribution of dispersal distances revealed that realised dispersal distances found within the study system were shorter than if individuals moved randomly between islands (Figure 5).

3.2 | Dispersal and population size

For farm islands, the proportion of emigrating recruits was smaller in populations with large mean population size, leading to the number of emigrants being independent of mean population size (Table 2). Moreover, on farm islands, immigration was proportional to the mean population size (Table 2; Table S4), resulting in a higher number of immigrating recruits with increasing mean population size of the island (Table 2; Table S4). On non-farm islands, the proportion emigrants among recruits was proportional to the long-term mean population size (β = 0.53, CI = −0.30, 1.36), resulting in a higher number of emigrants from populations with large mean population size (β = 2.08, CI = 0.79, 3.36). Thus, the patterns of long-term mean population size on emigration differed among habitat types (Table 2). However, the effect of mean population size on immigration was similar on non-farm islands, also showing immigration rates proportional to the mean population size (β = 0.01, CI = −1.14, 1.17), resulting in a higher number of immigrants into large mean population size also on non-farm islands (β = 1.45, CI = 0.20, 2.71).

We found no evidence for an effect of annual deviations from the mean population size on either the proportion of recruits emigrating or immigrating, or in the number of emigrants or immigrants (Table 2), but note a positive effect on immigration in years with population size above mean, in both habitats, when using a CMR integrating uncertainty in population estimates and recruiting probability from resighting probabilities (see, section 2; Table S9).

3.3 | Dispersal and recruit production

On the farm islands, the number of emigrants was negatively related to mean island recruit production (Table 3), but the proportion

emigrants was not dependent upon the mean production of recruits. Also, populations on farm islands with greater long-term mean recruit production had a lower number of immigrants, resulting in the proportion of recruits being immigrants was equal independent of long-term mean recruit production (Table 3). In contrast, on non-farm islands, the proportion and number of emigrants and immigrants were independent on the long-term average recruit production, thus, differed from the farm islands (Table 3; β = −0.05, CI = −0.62, 0.53; β = 0.95, CI = −0.90, 2.80; respectively).

When focusing on the effects of temporal fluctuations in recruit production on dispersal, on the farm islands in years when individual recruit production was higher, there was both a higher proportion and number of emigrating recruits (Table 3). For the non-farm islands, temporal fluctuations in the average recruit production did not affect the proportion of emigrating recruits (β = −0.07, CI = −0.31, 0.17), but affected the number of emigrating recruits (β = 0.35, CI = 0.08, 0.61). Though, farm and non-farm islands differed in both proportion and numbers of recruits emigrating in response to temporally high recruit production (Table 3). Despite a large effect of annual fluctuations in recruit production on emigration, no effect was found for proportions or numbers of immigrants in either habitat (Table 3). Note, however, that a positive effect of temporal recruit production on immigration proportion and numbers was found in both habitat types when using the extended CMR described in section 2 (i.e. properly integrating resighting data to estimate population size and recruiting probabilities; Table S10).

4 | DISCUSSION

This study shows that the spatio-temporal variation in emigration and immigration in this house sparrow system can be best characterized by a spatially explicit metapopulation structure (Hanski, 1999) depending upon the main type of habitat on each island. Furthermore, immigration into a given island population was influenced by the degree of isolation, and thus the exchange of individuals between nearby islands was higher (Tables 2 and 3; see also Tufto et al., 2005). Our results also show a link between dispersal and population dynamics, which differs as a function of habitat characteristics (Tables 2 and 3). The interactive effects on dispersal of population dynamics and habitat types (Tables 2 and 3) imply that simple metapopulation models, which do not include an explicit spatial structure, would fail to characterize the pattern of dispersal in this house sparrow metapopulation (Table 1).

4.1 | Spatial configuration

The negative effect of inter-island distance on emigration and immigration (Tables S2 and S3; especially in farm islands, see Table S4 and S6) has been shown to be a general feature of a metapopulation structure (see Hanski, 1998, 1999). Moreover, the mean proportion of dispersers among recruits in these local populations of house sparrows was far less than recorded in other avian metapopulations

TABLE 2 Results of mixed-effect models examining the annual proportion (A) and number (B) of emigrants and immigrants in a house sparrow metapopulation in northern Norway during the years 1993–2014. The mean distance to 10 other islands (island distance), habitat type (farm vs. non-farm islands), mean island population size (Mean pop. size), annual deviation from mean population size (deviation from mean pop. size) and the interactions between population size metrics and habitat type were included as fixed effects. For the fixed effects, we present mean and 95% credible intervals (CI: in parentheses) of the untransformed parameter estimates. The intercept represents the farm habitat. For the random effects, σ^2 and 95% CI (in parentheses) are presented. Fixed effect estimates where CI did not overlap zero (i.e. statistically significant) are depicted in bold. Italic-bold depicts trends (non-overlapping 90% CI, $n = 242$; 11 islands × 22 years)

	Emigration		Immigration	
	A	B	A	B
Fixed effects				
Intercept	−2.58 (−2.91, −2.26)	−1.06 (−1.59, −0.54)	−2.59 (−3.07, −2.11)	−0.92 (−1.46, −0.38)
Island distance	**−0.41 (−0.67, −0.15)**	**−0.51 (−0.90, −0.12)**	−0.16 (−0.54, 0.23)	−0.19 (−0.60, 0.22)
Habitat	**1.54 (1.05, 2.03)**	**2.33 (1.54, 3.13)**	**1.42 (0.65, 2.19)**	**0.83 (0.42, 1.24)**
Mean pop. size	**−0.54 (−0.78, −0.30)**	0.20 (−0.18, 0.58)	0.06 (−0.33, 0.45)	**2.06 (1.22, 2.89)**
Deviation from mean pop. size	−0.02 (−0.30, 0.25)	0.28 (−0.11, 0.66)	−0.09 (−0.30, 0.13)	0.14 (−0.18, 0.47)
Habitat: Mean pop. size	**1.07 (0.19, 1.94)**	**1.88 (0.53, 3.22)**	−0.05 (−1.26, 1.17)	0.62 (−0.68, 1.93)
Habitat: Deviation from mean pop. size	−0.15 (−0.82, 0.51)	−0.15 (−1.01, 0.71)	0.00 (−0.51, 0.51)	−0.06 (−0.77, 0.65)
Random effects				
Island	0.00 (0.00, 0.00)	0.15 (0.03, 0.72)	0.34 (0.13, 0.88)	0.30 (0.11, 0.81)
Year	0.00 (0.00, 0.00)	0.29 (0.10, 0.79)	0.00 (0.00, 0.00)	0.38 (0.18, 0.80)
Observation	0.37 (0.16, 0.85)	0.94 (0.68, 1.29)	0.20 (0.04, 1.12)	0.72 (0.52, 1.01)

TABLE 3 Results of mixed-effect models examining the annual proportion (A) and number (B) of emigrants and immigrants in a house sparrow metapopulation in northern Norway during the years 1993–2014. The mean distance to 10 other islands (island distance), habitat type (farm vs. non-farm islands), population growth, measured as the long-term mean average production of recruits per adult (Mean avg. rec. production) and annual deviation from the long-term mean (Dev. avg. rec. production) and the interaction between population growth and habitat type were included as fixed effects. For the fixed effects, we present mean and 95% credible intervals (CI: in parentheses) of the untransformed parameter estimates. The intercept represents the farm habitat. For the random effects, σ^2 and 95% CI (in parentheses) are presented. Fixed effect estimates where CI did not overlap zero (i.e. statistically significant) are depicted in bold. Italic-bold depicts trends (non-overlapping 90% CI, $n = 242$; 11 islands × 22 years)

	Emigration		Immigration	
	A	B	A	B
Fixed effects				
Intercept	−2.81 (−3.79, −1.84)	−1.69 (−2.68, −0.70)	−2.65 (−3.3, −2.01)	−2.12 (−3.4, −0.83)
Island distance	−0.31 (−0.76, 0.14)	**−0.64 (−1.10, −0.19)**	−0.22 (−0.47, 0.03)	**−0.71 (−1.33, −0.10)**
Habitat	**1.75 (0.44, 3.06)**	**2.58 (1.24, 3.92)**	**1.81 (1.05, 2.57)**	**3.31 (1.54, 5.09)**
Mean avg. rec. production	1.01 (−2.63, 4.65)	**−4.02 (−7.69, −0.34)**	−0.46 (−2.71, 1.78)	**−6.39 (−11.33, −1.45)**
Dev. avg. rec. production	**0.31 (0.05, 0.57)**	**0.76 (0.50, 1.03)**	−0.24 (−0.55, 0.07)	0.23 (−0.10, 0.57)
Habitat: Mean avg. rec. production	−0.85 (−4.79, 3.08)	**5.31 (1.33, 9.29)**	0.42 (−1.96, 2.80)	**7.34 (2.00, 12.68)**
Habitat: Dev. avg. rec. production	**−0.38 (−0.73, −0.02)**	**−0.42 (−0.79, −0.04)**	0.12 (−0.23, 0.48)	−0.03 (−0.47, 0.40)
Random effects				
Island	0.38 (0.17, 0.85)	0.36 (0.15, 0.84)	0.00 (0.00, 0.00)	0.56 (0.28, 1.13)
Year	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)
Observation	0.32 (0.11, 0.94)	0.56 (0.35, 0.89)	0.18 (0.03, 1.26)	0.65 (0.47, 0.92)

(Millon et al., 2019). This was probably due to a combination of the high degree of site fidelity in the house sparrow (Anderson, 2006) and the landscape structure of the study area, where the suitable habitat on islands is separated by sea, likely to decrease connectivity and limiting dispersal propensity (see Jensen et al., 2013). Similarly, dispersal rates in nuthatch *Sitta europaea* populations were lower in a

highly fragmented landscape than in a contiguous forest (Matthysen et al., 1995). We also found that most dispersal occurred between islands of the same habitat type (Table S8). The most important factor for the higher dispersal rates among islands within the same habitat type is probably that dispersal occurred mainly at shorter distances (Table S8; Tufto et al., 2005) and the distance between islands of the same habitat type was generally shorter, especially for farm islands (Figure 1).

4.2 | Spatial heterogeneity

A larger proportion and number of recruits dispersed within the non-farm islands (Figure 4a) compared to the farm islands, corroborating earlier findings of Pärn et al. (2012). Habitat-specific effects influencing dispersal may have profound effects on dispersal dynamics and viability of metapopulations. The studies of the metapopulation dynamics of the Glanville fritillary butterfly *Melitaea cinxia* on the Åland islands in Finland showed that spatial configuration and habitat quality were the major determinants of metapopulation persistence (Hanski et al., 2017), generally operating through an influence on movement among patches (Hanski, 2012; Harrison et al., 2011).

In addition, spatial variation in emigration and immigration rates in our house sparrow system was also explained by among-island differences in mean population size, but again we found habitat-specific patterns (Table 2, see also Tables S4–S7). Farm islands with larger mean population size produced a lower proportion of emigrating recruits, suggesting that individuals avoid leaving such populations. Similarly, in woodlands hosting collared flycatchers *Ficedula albicollis*, emigration was negatively related to population size (Doncaster et al., 1997). Reluctance to leave large populations may be caused by house sparrows being attracted to better, safer locations where there are more conspecifics (Stamps, 1988). The greater number of dispersers immigrating into populations on farm islands with larger mean population sizes further supports this idea of an effect of conspecific attraction in this system. A decrease in the proportion of emigrating recruits with increasing population size may also have contributed to the generally reduced emigration and immigration rates for the farm islands. This may have important consequences for the viability of small populations in this part of the metapopulation. The analyses of the spatial dynamics of the Glanville fritillary butterfly (Dallas et al., 2020; Hanski, 1999; Hanski et al., 2017), Acorn woodpeckers *Melanerpes formicivoru* (Stacey & Taper, 1992), American pika *Ochotona princeps* (Clinchy et al., 2002; Moilanen et al., 1998) and Scottish water voles *Arvicola amphibious* (Sutherland et al., 2014) have all provided evidence for metapopulation structures in which the persistence of local populations depends upon available immigrants and hence the probability of recolonization.

In contrast, mean house sparrow population size had a larger effect on the proportion as well as the number of individuals dispersing on the non-farm islands (Table 2; Table S5). Thus, large mean population size may indicate a mainland type of island contributing with emigrants and thereby sustain smaller surrounding populations, analogous to a mainland-island type of population structure (Table 1). This is in accordance with the results from an analysis of the structure of 42 Florida scrub jay (*Aphelocoma coerulescens*) metapopulations, where only three populations could be classified as a Levins (1969) type of structure that included subpopulations large enough to facilitate recolonization of surrounding habitat patches after extinction. In addition, five other metapopulations were considered to be of a mainland-island type in which local persistence depended upon immigration from a large source population, whereas the rest was either in non-equilibrium or had an intermediate (midland-island) metapopulation structure (Stith et al., 1996), the latter matching what we found for the non-farm habitat type.
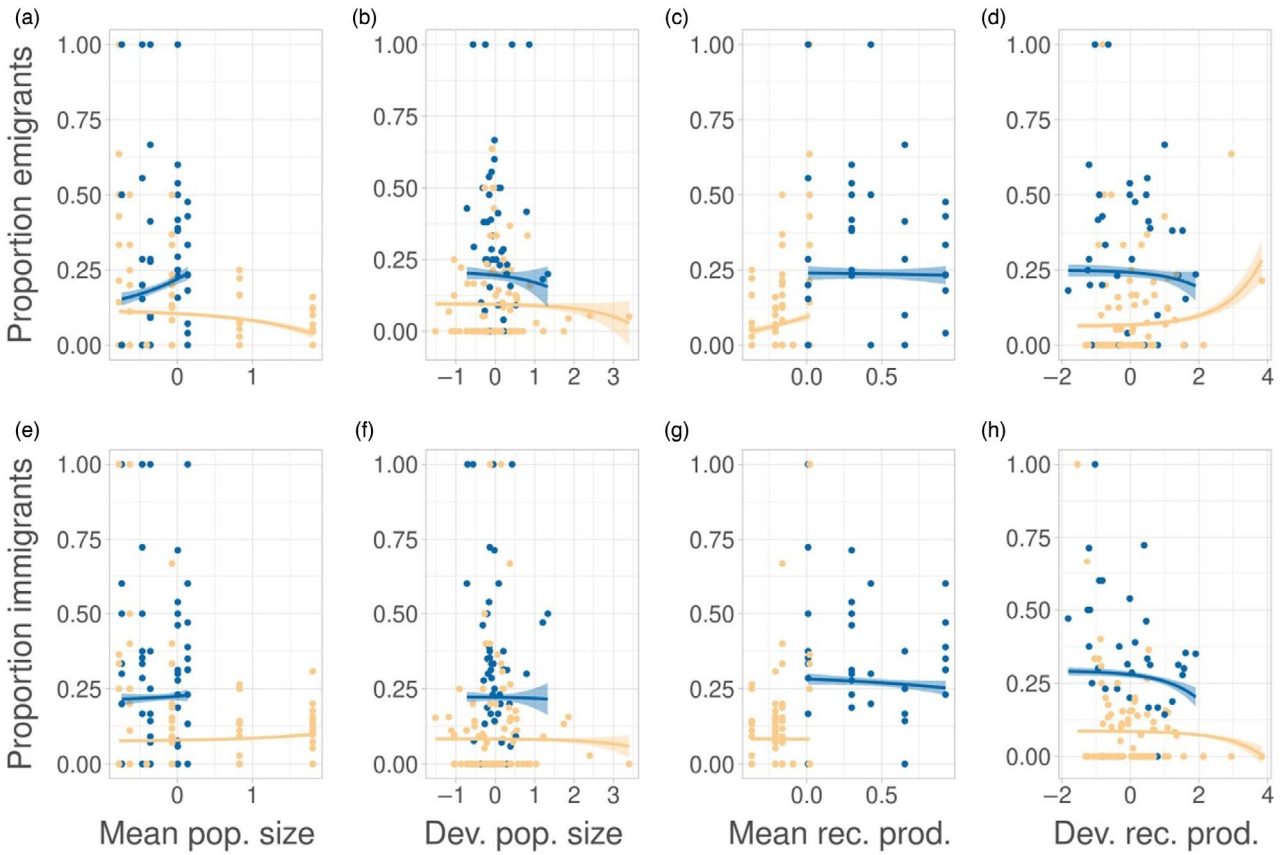
In both habitat types, immigration proportion and numbers were positively associated with larger mean population sizes (Table 2). For farm islands, increased immigration to larger mean population sizes might have been expected under conspecific attraction (Stamps, 1988), but on non-farm island, it was not expected according to the mainland-island type of dispersal, where small populations would be expected to receive more immigrating recruits (Table 1). Thus, immigration was more dependent upon geographical isolation and mean population size. These results imply that populations with large mean population sizes may have been associated with relatively higher quality habitats, or were favoured due to Allee (1931) effects and/or conspecific attraction (Stamps, 1988).

For recruit production, populations on farm islands with a large long-term production of recruits had a greater number of emigrants, leading to equal proportions of recruits emigrating independent on the long-term average recruit production (Tables 3; Table S6). This again supports the idea that recruits were reluctant to leave generally productive populations, in accordance with the characteristics of the balanced dispersal (Doncaster et al., 1997) and conspecific attraction (and attraction to conspecific reproduction) metapopulation models (Doligez et al., 2002; Stamps, 1988; Table 1). However, immigration tended to be greater into populations producing consistently fewer recruits per adult on farm islands (Table 2; Table S6), which is more in accordance with source–sink dynamics (Pulliam, 1988, 1996; Pulliam & Danielson, 1991). Moreover, it may as well be that immigration occurred independent of recruit production, and that more productive populations directly affect the proportion recruits being resident.
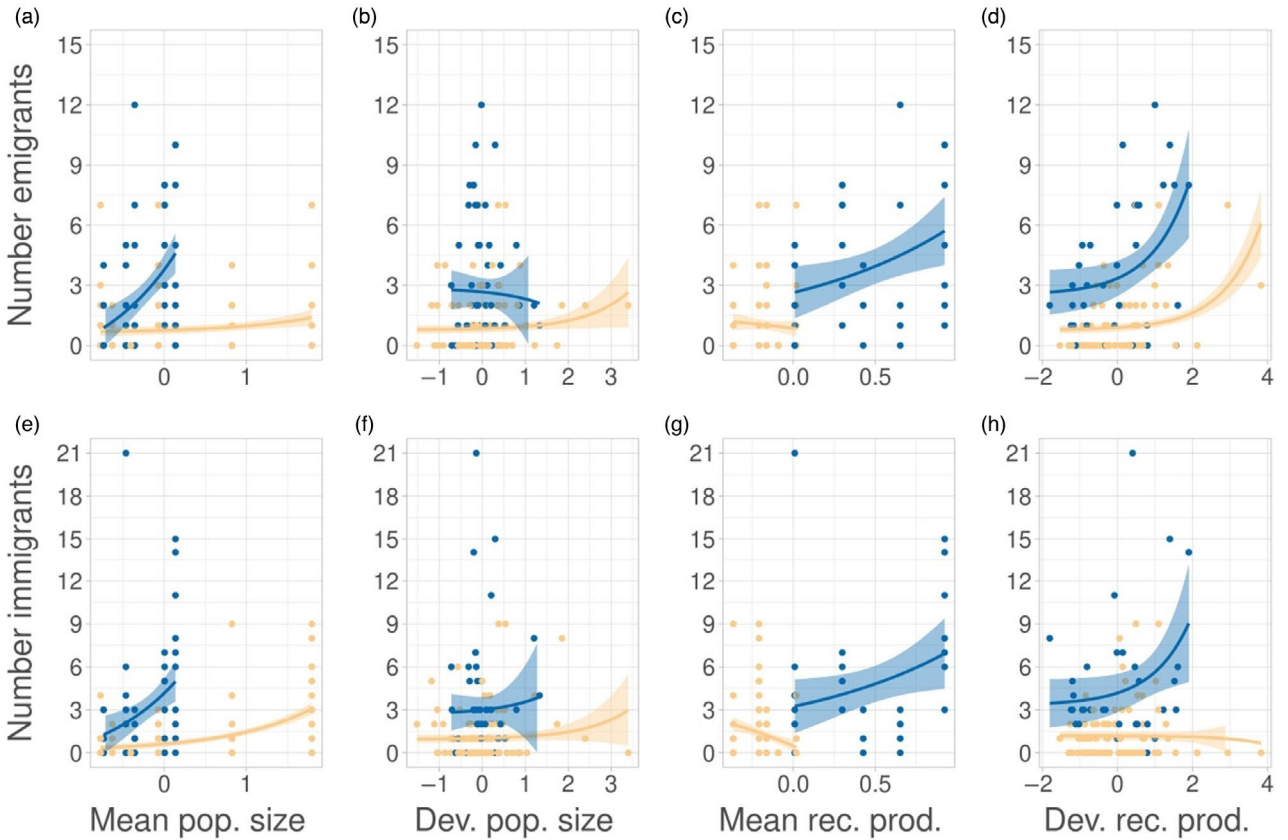
4.3 | Local population dynamics

Temporal fluctuations in local population sizes did not affect the proportion or number of emigrants or immigrants (Table 2), indicating density-independent dispersal rates in this metapopulation. It may as well suggest that the estimates of deviations from the mean adult population size are poor measures of the processes driving temporal fluctuation in population dynamics, see for example the effect in Pärn et al. (2012) using population sizes including juveniles as a measure of density. Alternatively, short-term fluctuations in
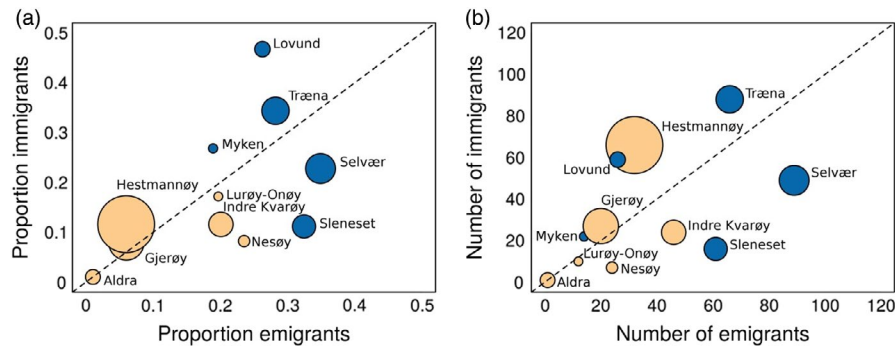
Proportion

Number

FIGURE 4   Relationships between proportion of recruits being emigrants versus immigrants (a), and the number of emigrants versus
immigrants (b) of house sparrows at the 11 islands (circle colours indicate habitat type; blue: non-farm islands; beige: farm islands). Size of
dots indicates the mean number of recruits produced. The dashed diagonal represents the 1:1 relationship

adult population size may not be so important for dispersal deci-
sions, with individuals instead relying on cues that reflect long-term
habitat quality (as reflected in our measures of mean population size
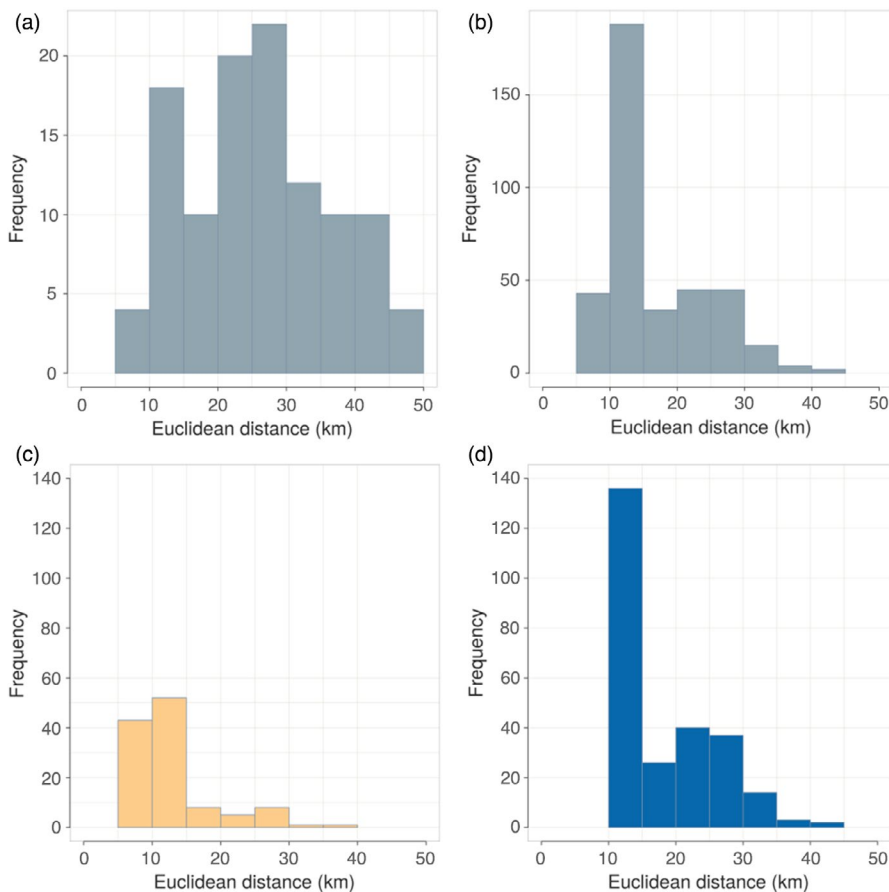per island).

Actually, for the farm islands in years when recruit production
was above average, both the proportion and number of emigrating
recruits increased (Table 3; Table S6). On non-farm, only the number
of emigrants increased in years with large recruit production, but
only proportional to the recruit production (Table S7). Thus, temporal
increased recruit production led to more emigration in both habitat
types, particularly in farm islands (Table 3), resembling source–sink
dynamics (Pulliam, 1988, 1996; Pulliam & Danielson, 1991). Increased
emigration rates in years with large offspring production could be
related to density-dependent effects acting on recruits, for exam-
ple due to increased resource competition (Bowler & Benton, 2005;
Matthysen, 2005). The difference in the relationship between local
population dynamics and dispersal will consequently affect the pat-
terns of dispersal dynamics at the metapopulation level. Importantly,
the combined effects of local demography and environmental sto-
chasticity generates substantial annual variation in the number of
dispersing individuals in the metapopulation (see Figure 3).

4.4 | Metapopulation models

Taken together, the geographic isolation and spatial differences in
mean population size had a substantial effect on house sparrow
emigration and immigration in both habitats, suggesting the need
for spatially explicit metapopulation models (Table 1). Moreover,

variation in mean population size and recruit production affected
dispersal dynamics differently, depending upon habitat type
(Tables 2 and 3). Although some features of the dispersal dynamics
corresponded to specific assumptions in different metapopulation
models (Table 1), these models still failed to describe dispersal dy-
namics consistently for emigration and immigration in both habitat
types. Similar challenges in characterizing dispersal dynamics for
whole metapopulations have been found in species like the Florida
scrub jay (Stith et al., 1996). This may be related to the size of the
studied metapopulations relative to movement abilities for the spe-
cies under study, emphasizing the importance of scale. In this study,
we covered a large geographical area compared to mean dispersal
distance (Tufto et al., 2005), which may have resulted in spanning
over two largely independent subsystems with their own dynam-
ics. This is further highlighted by the low exchange of individuals
between farm- versus non-farm habitat (Table S8), likely contribut-
ing to general morphological differences among these parts of the
metapopulation (Araya-Ajoy et al., 2019).

This study involves the natal dispersal of individuals born within
the house sparrow metapopulation. Although the site of origin of
a large fraction of individuals present on these islands is known
(Saatoglu et al., 2021), unringed individuals still appear each autumn.
Whether these individuals are unringed offspring from undetected
or inaccessible nests or long-distance immigrants from outside the
study area is currently unknown, which means that we cannot fully
assess the importance of a mainland-island type (Table 1) of disper-
sal in this analysis. However, the genetic assignment of individuals
with unknown origin indicated that it was unlikely that these individ-
uals were long-distance dispersers (Saatoglu et al., 2021).

FIGURE 5 Frequency histograms of all pairwise distances between the 11 study islands in the house sparrow metapopulation (a); distances of all recorded inter-island dispersal events (b), where individuals emigrated from farm islands (c) and from non-farm islands (d)

5 | CONCLUSIONS

Dispersal in this house sparrow metapopulation strongly depends upon geographical isolation and habitat characteristics interacting with spatial variation in population size and temporal variation in individual recruit production. This study emphasises the need for analyses addressing how spatial features of the environment affecting variation in emigration and immigration interact with the factors affecting temporal fluctuations in local population dynamics in order to predict the persistence capacity of metapopulations (Dallas et al., 2020, 2021; Hanski & Ovaskainen, 2000).

CONFLICT OF INTEREST
The authors declare that there is no conflict of interest.

AUTHORS' CONTRIBUTIONS
B.-E.S., T.H.R., H.J. and H.P. conceived the initial idea; P.S.R. and Y.G.A.-A. further developed hypotheses, performed the statistical analysis, interpreted the results and wrote the paper, with critical input from all authors. All authors contributed to the data collection and gave final approval for publication.

DATA AVAILABILITY STATEMENT
Data associated with this study are made available in the Dryad Digital Repository https://doi.org/10.5061/dryad.v41ns1rx1 (Ranke et al., 2021).

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