

Landscape genetic analyses reveal fine-scale effects of forest fragmentation in an insular tropical bird

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Abstract

Within the framework of landscape genetics, resistance surface modelling is particularly relevant to explicitly test competing hypotheses about landscape effects on gene flow. To investigate how fragmentation of tropical forest affects population connectivity in a forest specialist bird species, we optimized resistance surfaces without a priori specification, using least-cost (LCP) or resistance (IBR) distances. We implemented a two-step procedure in order (i) to objectively define the landscape thematic resolution (level of detail in classification scheme to describe landscape variables) and spatial extent (area within the landscape boundaries) and then (ii) to test the relative role of several landscape features (elevation, roads, land cover) in genetic differentiation in the Plumbeous Warbler (*Setophaga plumbea*). We detected a small-scale reduction of gene flow mainly driven by land cover, with a negative impact of the nonforest matrix on landscape functional connectivity. However, matrix components did not equally constrain gene flow, as their conductivity increased with increasing structural similarity with forest habitat: urban areas and meadows had the highest resistance values whereas agricultural areas had intermediate resistance values. Our results revealed a higher performance of IBR compared to LCP in explaining gene flow, reflecting suboptimal movements across this human-modified landscape, challenging the common use of LCP to design habitat corridors and advocating for a broader use of circuit theory modelling. Finally, our results emphasize the need for an objective definition of landscape scales (landscape extent and thematic resolution) and highlight potential pitfalls associated with parameterization of resistance surfaces.

KEYWORDS

gene flow, landscape connectivity, optimization, tropical island

1 | INTRODUCTION

Habitat fragmentation—a landscape process involving both habitat loss and the breaking apart of habitat (Fahrig, 2003)—is one of the most severe threats to biodiversity and therefore a major research theme in ecology and conservation biology (Fahrig, 2003; Fischer & Lindenmayer, 2007; Lindenmayer et al., 2008). Subdivision and

isolation of habitat patches may lead to a reduction in population size and dispersal with negative genetic consequences for fragmented populations, although response level may vary depending on species (Keyghobadi, 2007; Radespiel & Bruford, 2014). The reduction of within-population genetic diversity and the increase of genetic differentiation among previously connected populations that are expected can have negative effects on the long-term persistence

of fragmented populations and ultimate modifications of species evolutionary trajectory (Frankham, 2005; Keyghobadi, 2007; Khimoun, Eraud, et al., 2016; Radespiel & Bruford, 2014). Thus, understanding how landscape characteristics affect dispersal and population connectivity is crucial in assessing the consequences of habitat fragmentation and in targeting conservation priorities (Tschamntke et al., 2012).

By combining landscape ecology, population genetics and spatial statistics, landscape genetics offers a unique framework to infer landscape-genetics relationships, especially to understand how landscape features enhance or impede population connectivity (Balkenhol, Cushman, Storfer, & Waits, 2016; Balkenhol, Waits, & Dezzani, 2009; Holderegger & Wagner, 2008; Manel & Holderegger, 2013; Manel, Schwartz, Luikart, & Taberlet, 2003; Segelbacher et al., 2010). Within this framework, resistance surfaces (i.e., spatial layers whose values represent the extent to which conditions at each grid cell constrain gene flow) are particularly relevant to explicitly test competing hypotheses about landscape effects on gene flow (Balkenhol et al., 2016; Spear, Balkenhol, Fortin, Mcrae, & Scribner, 2010). However, methods for conducting landscape resistance analyses continue to evolve and develop, with no consensus about the best practices for modelling resistance surfaces (Spear et al., 2010; Zeller, McGarigal, & Whiteley, 2012). As a consequence, their parameterization (i.e., assigning a value of resistance to each environmental condition) and analysis pose significant challenges (Richardson, Brady, Wang, & Spear, 2016).

Expert opinion and empirical data (e.g., presence/absence, abundance and experimental movement) are the two alternative approaches used to parameterize resistance surfaces. Empirical approaches to the parameterization of resistance surfaces are becoming increasingly popular, as they do not suffer from the subjectivity of expert opinion that may have serious consequences on landscape genetic inferences (Beier, Majka, & Newell, 2009; Charney, 2012; Pérez-Espona et al., 2008; Rayfield, Fortin, & Fall, 2009). However, resistance surfaces derived from habitat suitability models or resource selection functions may also lead to erroneous conclusions of landscape-genetics relationships, as species ecological requirements do not necessarily reflect processes driving gene flow (Balkenhol et al., 2016; Peterman, Connette, Semlitsch, & Eggert, 2014).

Another important, and often overlooked, issue in empirical studies is the mismatch between the scale of research and the scale of processes governing gene flow (Richardson et al., 2016). Indeed, simulation studies have found that incorrect specification of thematic resolution (i.e., level of detail in classification scheme to describe landscape variables) and spatial extent (i.e., area within the considered landscape boundaries) of the landscape may substantially affect the strength and nature of landscape-genetics pattern-process relationships (Cushman & Landguth, 2010a). Because accurate landscape genetic inferences are dependent upon correct specification of landscape scales and resistance values, methods developed to optimize resistance surfaces by simultaneously considering multiple resistance surfaces and exploring an unbounded range of cost values without a

priori specification seem promising to alleviate subjectivity and uncertainty in parameterization (Peterman et al., 2014; Richardson et al., 2016; Ruiz-Lopez et al., 2016). Here, we conducted a landscape genetics analysis following an approach of resistance surface optimization based on an objective definition of the landscape extent and resolution, in order to assess the influence of tropical forest fragmentation on gene flow in a forest specialist bird species in Guadeloupe Island.

Tropical forests are the terrestrial habitat harbouring the highest biodiversity (biodiversity hotspot; Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000), but they are also currently experiencing the highest rates of habitat loss and fragmentation (Hansen, Stehman, & Potapov, 2010; Laurance, 2010). Therefore, there is an urgent need to better understand how forest fragmentation affects biodiversity in tropical areas in order to anticipate and limit its negative consequences. However, the vast majority of landscape genetics studies focus on temperate locations and tropical environments remain understudied (Storfer, Murphy, Spear, Holderegger, & Waits, 2010). In addition, negative effects of habitat loss and fragmentation are especially critical in insular systems that tend to harbour high levels of endemism and where physical boundaries and geographic isolation constrain species' movements, preventing recurrent gene flow from outside (Brooks et al. 2002; Cincotta, Wisniewski, & Engelman, 2000; Whittaker & Fernandez-Palacios, 2007). Guadeloupe is a small island (1,450 km²) in the Lesser Antilles and forest habitat covers 44% of the island, making this island the most forested French Overseas Region after French Guiana (IGN Institut National de l'Information Géographique et Forestière, 2014). Guadeloupe Island is divided into two zones, Basse-Terre on the west side (BT, about 850 km²) and Grande-Terre on the east side (GT, 600 km²), connected by a narrow isthmus (Figure 1). Forest fragmentation mainly results from the development of urban areas and agricultural surfaces, which have been dominated by sugar cane plantations since the mid-18th century (Conseil Régional de Guadeloupe 2013).

Although birds have long been regarded as less sensitive to habitat fragmentation than other taxa because of their assumed high dispersal abilities, recent works have shown that gene flow can be restricted over very short geographic distances in avian species (Arnoux et al., 2014; Bertrand et al., 2014; Khimoun, Arnoux, et al., 2016; Khimoun, Eraud, et al., 2016). In addition, a previous study based on the comparison of a continuous forest and a fragmented forest within a small island revealed that forest fragmentation affects population genetic structure in several bird species at a small spatial scale and that forest specialist species are more impacted than co-occurring generalist species (Khimoun, Eraud, et al., 2016). We thus investigated the consequences of forest fragmentation on gene flow in a forest specialist bird species (Khimoun, Eraud, et al., 2016), the Plumbeous Warbler *Setophaga plumbea*, foraging mostly in understory and endemic from Guadeloupe and Dominica Islands (Lesser Antilles; Curson, 2017). Overcoming the binary description of landscape (i.e., opposing suitable habitat and inhospitable matrix) deeply rooted in the Island biogeography theory (MacArthur & Wilson, 1963, 1967), we adopted a mosaic-like description of the landscape

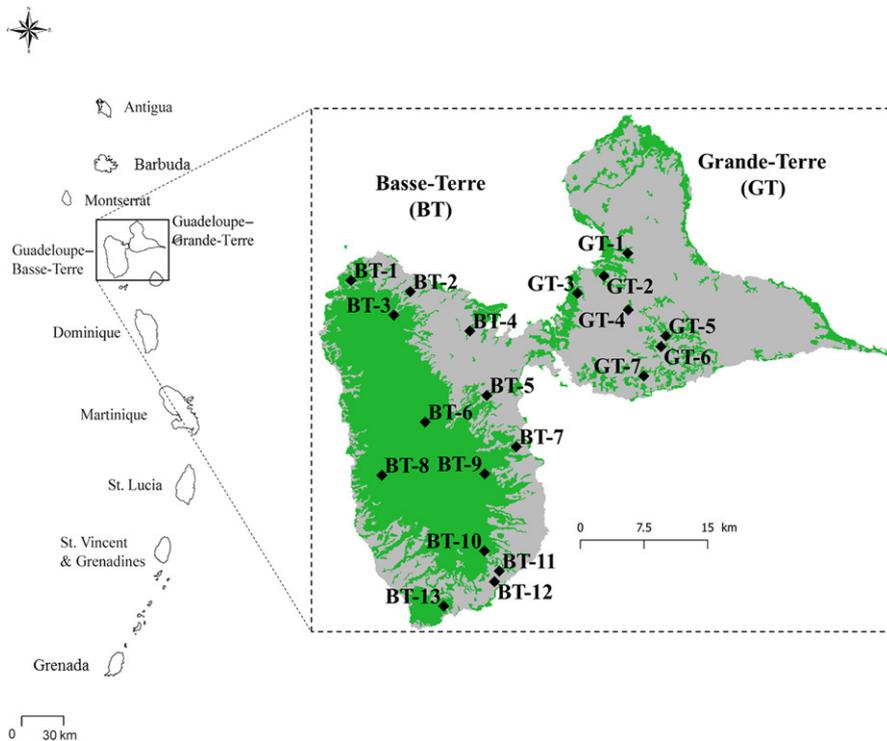


FIGURE 1 Populations sampled across the Guadeloupe Island. The forest habitat, nonforested land surfaces and the sea are represented in green, grey and white, respectively. Sampled sites on Basse-Terre (BT-) and on Grande-Terre (GT-) are indicated by diamonds [Colour figure can be viewed at wileyonlinelibrary.com]

to further investigate the potential effect of matrix composition and configuration in mitigating consequences of forest fragmentation on population connectivity (Ricketts, 2001). We tested the relative performances of Euclidian distances and ecological distances, integrating both anthropogenic and natural landscape features (i.e., elevation, roads and land cover type), to explain population genetic differentiation. Although elevation was shown to reduce gene flow in amphibians and small mammals, its effect in birds is not clear, with both negative and no effects reported in previous studies (Storfer et al., 2010). Roads constitute a strong barrier to gene flow in several organisms, including birds that may exhibit reluctance to cross roads that are 10–30 m wide (Develey & Stouffer, 2001). We thus expect a negative influence of the road network on gene flow in the Plumbeous Warbler. Finally, as habitat loss and fragmentation may negatively affect population connectivity in specialist species, we expect all nonforested surfaces to reduce gene flow in the studied species, and the quantification of the relative impacts of different anthropogenic land cover types (i.e., urban and agricultural areas, meadows) is one of the main purposes of this study.

As little is known about natural history in most tropical birds (Stutchbury & Morton, 2001), including the Plumbeous Warbler, approaches of resistance surface optimization without a priori specification of cost values are particularly relevant. We used the method of resistance surface optimization developed by Peterman et al. (2014) and Peterman (2014) that we implemented in a two-step procedure in order (i) to objectively define landscape scales (thematic resolution and spatial extent) and then (ii) to test which anthropogenic and natural landscape features (elevation, land cover and roads), independently or in combination, best explain genetic differentiation. As they rely on different assumptions about animal

landscape perception during dispersal, we used two different approaches to compute ecological distances. On the one hand, the least-cost distance was calculated as the cumulative cost associated with traversing the least-cost path connecting each population pair (Adriaensen et al., 2003). On the other hand, the resistance distance, a graph-theoretic distance metric based on circuit theory, was calculated by simultaneously considering all possible paths connecting each population pair (McRae, 2006). We assessed the relative support of three competing causal models of isolation corresponding to (i) the isolation-by-distance hypothesis (IBD model), which proposes that gene flow is a function of Euclidian distance among populations, and the landscape connectivity hypotheses, which propose that gene flow is a function of ecological distance relying on (ii) the least-cost distance (LCP model) or (iii) the resistance distance (IBR model). To this aim, we compared the relative abilities of Euclidian, least-cost and resistance distances to explain gene flow in our study system, providing insights into dispersal behaviour of this species and raising potential implications for conservation measures.

2 | MATERIAL AND METHODS

2.1 | Sampling and molecular analyses

Birds were mist-netted in 20 sites located within forest patches on the island of Guadeloupe (13 sites in Basse-Terre (BT) and seven sites in Grande-Terre (GT); Figure 1). Each bird was banded to prevent resampling and 20 μ l of blood was collected from the brachial vein using sterile needles and heparinized tubes, in conformity with legal requirements in France (see Acknowledgements). Blood samples were stored in 500 μ l of QLB (Queen's lysis buffer), and birds were

released at their capture location. Total DNA extraction was performed following a standard phenol–chloroform protocol (optimized from Hillis, Moritz, and Mable (1996)), from 240 μ l of blood in QLB after a first step of proteinase K digestion (overnight incubation at 55°C). Individuals were genotyped with twelve microsatellites (Appendix S1) following PCR conditions outlined in Ref. (Khimoun, Arnoux, et al., 2016; Khimoun, Eraud, et al., 2016). Loci were amplified in simplex in a Dyad thermal cycler (Bio-Rad, Hercules, CA, USA), PCR products were multiloading for analyses in an automated sequencer (ABI3730), and allele scoring was performed with GENEIOUS R.8 (Kearse et al., 2012).

2.2 | Population genetics analyses

Preliminary tests for linkage disequilibrium between pairs of loci and tests for deviation from Hardy–Weinberg expectations were performed within each population, using GENEPOP 4.3 (Rousset, 2008). Within-population diversity was assessed by observed (H_O) and expected (H_E) heterozygosity calculated in GENETIX (Belkhir, Chikhi, Raufaste, & Bonhomme, 2004) and by standardized allelic richness (A) and standardized private allelic richness (PrA) estimated using a rarefaction method implemented in ADZE 1.0 (Szpiech, Jakobsson, & Rosenberg, 2008), and all four metrics were averaged over loci. Levels of within-population diversity were compared between populations from BT and GT, because these two parts of Guadeloupe Island host a differentiated gene pool.

Population genetic structure was first assessed using a Bayesian model-based clustering algorithm implemented in STRUCTURE 2.3.4 (Pritchard, Stephens, & Donnelly, 2000). We tested for the presence of K genetic clusters, K ranging from 1 to 20 (the number of sampled localities). We used an admixture model (Falush, Stephens, & Pritchard, 2003) with correlated allele frequencies, without LocPrior (Hubisz, Falush, Stephens, & Pritchard, 2009). We performed 10 independent runs of 100,000 iterations following a burn-in period of 20,000 iterations. The number of genetic clusters was inferred following the approach proposed by Garnier, Alibert, Audiot, Prieur, and Rasplus (2004), focusing on successive increases of posterior probability of the data (IPPD) for increasing values of K . We also tested for genotypic differentiation both over all populations and between all pairs of sampled populations using a log-likelihood based exact G -test. Significance was adjusted using Bonferroni correction when multiple tests were performed. Levels of differentiation were quantified by global and pairwise estimates of F_{ST} following Weir and Cockerham (1984), using GENEPOP (Rousset, 2008).

2.3 | Landscape genetics analyses

2.3.1 | General framework of resistance surface optimization

To test the hypothesis of landscape resistance on gene flow, we followed the framework of optimization and selection of resistance surfaces developed by Peterman et al. (2014) and implemented in the R

package RESISTANCEGA version 2.0-16 (Peterman, 2014; <https://github.com/wpeterman/ResistanceGA>). Briefly, this method optimizes resistance surfaces using genetic algorithms, seeking to maximize the relationship between pairwise landscape resistances or least-cost distances and pairwise genetic distances. Continuous and categorical resistance surfaces were iteratively and independently optimized from (i) pairwise resistance distances calculated in CIRCUITScape (McRae, Dickson, Keitt, & Shah, 2008), and (ii) pairwise least-cost distances calculated from least-cost path using the R package GDISTANCE (Van Etten, 2014). The objective function during optimization was AIC, which was determined from linear mixed-effects models fit with pairwise F_{ST} as the dependent variable and the scaled and centred resistance or least-cost distance between population pairs as the predictor variable. Mixed models were fitted using the maximum-likelihood population effects (MPLE) parameterization (Clarke, Rothery, & Raybould, 2002) implemented in the R package LME4 (Bates, Maechler, Bolker, & Walker, 2014) in order to account for the nonindependence among the pairwise genetic and ecological distances. Support for optimized resistance surfaces was assessed using AICc (Akaike information criteria corrected for small sample size).

2.3.2 | Landscape variables and definition of optimal landscape scales

Description of landscape variables

We assessed the influence of three landscape variables on population connectivity: (i) land cover (25-m categorical map of land cover classes, CORINE Land Cover 2006; <http://www.statistiques.developpement-durable.gouv.fr>), (ii) road network (25-m categorical map including presence/absence of a road; BD TOPO[®] v2 IGN) and (iii) elevation (continuous surface derived from a 25-m digital elevation model, BD TOPO[®] v2 IGN; Figure 2). As changing grain size (i.e., pixel size) does not have a large effect on the detection of landscape-genetic associations (Cushman & Landguth, 2010a; McRae et al., 2008), no preliminary analysis was conducted to define the optimal grain size and landscape surfaces were resampled to a lower spatial resolution of 100 m \times 100 m cell size, ensuring a reasonable computation time. More importantly, preliminary analyses were conducted to determine (i) the optimal spatial extent and (ii) the optimal thematic resolution of the landscape, as their incorrect specification may have serious consequences on landscape genetics inference (Beier et al., 2009; Cushman & Landguth, 2010a; Rayfield et al., 2009).

Construction of landscape surfaces relying on alternative definitions of spatial extent and thematic resolution

Defining the landscape extent relevant for landscape genetics studies may seem trivial when working on terrestrial organisms within an island. However, this might be complicated by the fact that some organisms such as birds have potential high intrinsic dispersal abilities but paradoxically strong behavioural barriers to dispersal (Harris & Reed, 2002). Thus, a priori decisions to include/remove sea pixels

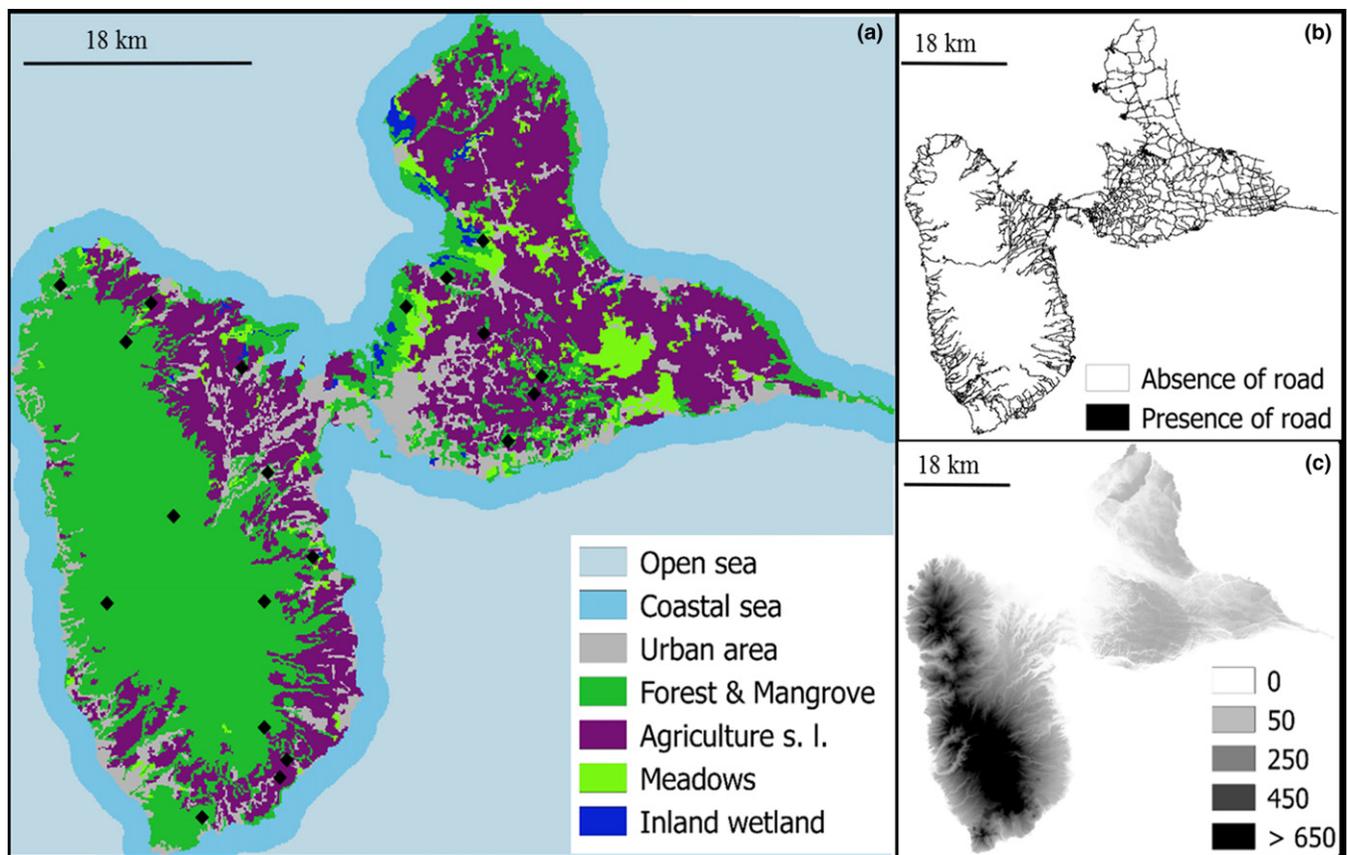


FIGURE 2 Landscape surfaces used to calculate LCP and resistance distances. (a) Categorical land cover surface encompassing five different land cover classes and two different classes describing the sea (this surface originates from preliminary analyses used to define the optimal landscape scales); (b) Categorical road surface encompassing two classes: presence (black) and absence of road (white); (c) Continuous elevation surface (in metres). All these landscape surfaces have a spatial resolution of $100\text{ m} \times 100\text{ m}$ cell size [Colour figure can be viewed at wileyonlinelibrary.com]

from the landscape windows (in other words, allowing/preventing overseas dispersal) seem a strong assumption, especially when considering the convex shape of the Guadeloupe Island. Indeed, gene flow between Basse-Terre and Grande-Terre (the two parts of the island) may occur by bird dispersal through the isthmus connecting these parts of the island, but it may also occur by overseas dispersal. Consequently, two alternative land cover surfaces were generated for preliminary analyses to determine the landscape extent: one is excluding and the other one is including pixels of sea from the landscape windows (Figure 3a,b, respectively).

Dispersal involves two different steps: crossing the boundary between the suitable habitat and the matrix and then dispersal through the matrix. In order to account for these two steps during potential overseas dispersal events, we adopted a finer thematic resolution for the sea by defining two different classes: the “coastal sea” included within a 1.5-km buffer surrounding the island and representing the transition area between the land and the “open sea” located beyond this buffer. A third land cover surface was built following this finer thematic resolution (Figure 3c). One additional land cover surface was built by removing the open sea from the landscape windows (Figure 3d), thus preventing population

connection through pixels of “open sea” during optimization of resistance surfaces. Finally, based on the best-supported landscape extent and thematic resolution of the sea, we further investigated the thematic resolution of agriculture surfaces in terms of vegetation structure which may influence the decision to move through the matrix (Prevedello & Vieira, 2009). Thus, we constructed one additional land cover surface grouping agricultural area, banana and sugar cane plantations into a single class, named “Agriculture s. l.” (Figure 3e).

Preliminary analysis to objectively define the optimal landscape scales

A total of five alternative surfaces were thus developed (Figure 3) and resistance surfaces were optimized for each of them. Ten independent runs of optimization were conducted for each surface to assess the convergence in parameter estimates. AIC values were used as the objective criteria to compare models and to select landscape surfaces that provided the optimal definition of landscape scales (i.e., thematic resolution and spatial extent) for the following analyses. Because of computation limitation, these 50 preliminary runs of optimization were only conducted using least-cost distance.

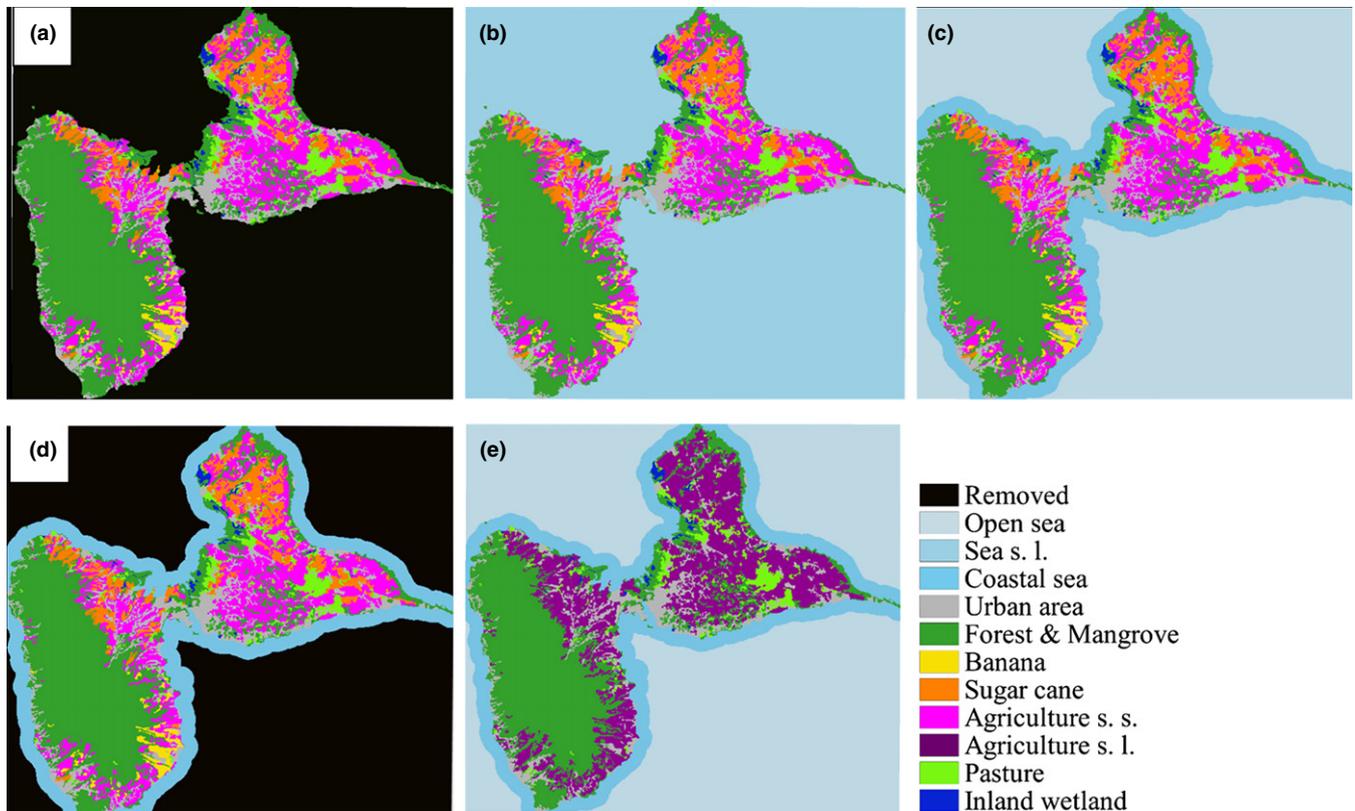


FIGURE 3 Alternative land cover surfaces considered to objectively define the spatial extent and the thematic resolution of the landscape. (a) Land cover surface removing sea pixels from the landscape window; (b) Land cover surface including sea pixels described by a single class within the landscape window; (c) Land cover surface including sea pixels described by two different classes: the “coastal sea” included within a 1.5-km buffer surrounding the island and the “open sea” located beyond this buffer; (d) Land cover surface excluding the “open sea” from the landscape window defined in (c); (e) Land cover surface grouping agricultural area “Agriculture s. s.,” “banana” and “sugar cane” plantations into a single class, named “Agriculture s. l.” and including the two classes of sea defined in C in the landscape window [Colour figure can be viewed at wileyonlinelibrary.com]

2.3.3 | Univariate/multivariate optimization of resistance surfaces

Univariate optimization was conducted for each of the three landscape surfaces (land cover, roads and elevation) defined from preliminary analysis, using both least-cost and resistance distances. In addition, the three surfaces were optimized simultaneously to generate a composite resistance surface. During multisurface optimization, each surface is iteratively modified, as in univariate optimization, but all resistance surfaces are then summed to create a single composite surface over which least-cost and resistance distances are calculated. Five independent runs were conducted for each univariate and multivariate optimization and resistance values were rescaled from 1 to 1,000 to allow comparison across replicates.

2.3.4 | Relative performances of geographic and ecological distances

Definition of geographic and ecological distances

We compared the ability of the three competing models of isolation in predicting genetic differentiation in the Plumbeous Warbler:

isolation by distance (IBD), least-cost path (LCP) or isolation by resistance (IBR). To this aim, we tested correlations between the pairwise genetic distances and geographic or ecological distances. For IBD, the log-transformed Euclidian distance was used as the geographic distance between populations. For LCP, the least-cost distance was calculated as the cumulative cost associated with traversing the least-cost path connecting each population pair (Adriaensen et al., 2003). Finally, IBR was based on the resistance distance, a graph-theoretic distance metric based on circuit theory that was calculated by simultaneously considering all possible paths connecting each population pair (McRae, 2006). The least-cost distance assumes that organisms disperse following a single and optimal route (i.e., least-cost path), whereas the resistance distance accounts for the possibility that multiple movement pathways between sites can enhance gene flow (McRae, 2006; McRae et al., 2008). For LCP and IBR, correlations were based on ecological distances resulting from the best-supported resistance surfaces.

Test of competing models

The three models were compared following a causal modelling approach developed by Cushman, McKelvey, Hayden, and Schwartz

(2006). In this framework, the best-supported model should exhibit the highest simple correlation with genetic distance, but also a significant positive partial correlation with genetic distance after controlling for the effect of the competing models (McRae & Beier, 2007). Although the use of partial Mantel tests has been controversial as they suffer from high rates of type I error (Castellano & Balleto, 2002; Raufaste & Rousset, 2001), simulation has demonstrated the very high power of these tests, when used in a causal modelling framework, to reject the incorrect causal model and to correctly identify the model driving the observed pattern of genetic differentiation (Cushman & Landguth, 2010b; Cushman, Wasserman, Landguth, & Shirk, 2013). Significance of correlations and partial correlations was tested using Mantel and partial Mantel tests implemented in R using the *partial.mantel.test* function in the R package NCF (Bjornstad, 2013), with 10,000 random permutations. Finally, based on the best-supported model (see Results), current flows among sampled locations were visualized using CIRCUITSCAPE (McRae et al., 2008).

3 | RESULTS

3.1 | Locus reliability and within-population genetic diversity

A total of 432 individuals were captured over the 20 sampling sites. All loci were in Hardy–Weinberg equilibrium: 13 tests (involving nine different loci in ten different populations) over a total of 236 tests performed were significant at the 0.05 level and none remained significant after Bonferroni correction. Only 72 tests (6%) of linkage disequilibrium over 1,188 tests performed (population/locus pair combinations) were significant at the 0.05 level, and five tests (0.4%) involving different locus pairs in different populations remained significant after Bonferroni correction. Therefore, the twelve microsatellite loci used were statistically independent. The number of alleles observed per locus ranged from five to 23 (mean = 14.2 ± 7.5) and the proportion of missing genotypes ranged from 0% to 7.4% (mean = $1\% \pm 2\%$, Appendix S1). Within populations, observed heterozygosity and expected heterozygosity, respectively, ranged from 0.611 and 0.649 to 0.761 and 0.735 (Table 1). Standardized allelic richness (A) and standardized private allelic richness (PrA) averaged over loci ranged from 4.145 to 5.277 and from 0.022 to 0.263, respectively (Table 1). Based on these four measures, no difference in levels of genetic diversity was detected between populations from BT and from GT (Mann–Whitney *U* tests; $p > .12$ for all tests).

3.2 | Population genetic structure

We found significant global genetic differentiation among sampled populations (overall $F_{ST} = 0.037$; $p < .001$). From STRUCTURE algorithm, the increase of posterior probability of the data was maximized at $K = 2$ (IPPD = 393), revealing two main differentiated gene pools (Figure 4 and Appendix S2-A). Populations from BT

TABLE 1 Estimates of intrapopulation genetic diversity

Location	Sites	N	H_E	H_O	A	PrA
Basse-Terre	BT-1	6	0.652	0.611	4.417	0.099
	BT-2	23	0.705	0.761	4.705	0.111
	BT-3	19	0.730	0.702	4.988	0.132
	BT-4	12	0.674	0.705	4.299	0.079
	BT-5	25	0.671	0.670	4.571	0.094
	BT-6	28	0.710	0.666	4.970	0.169
	BT-7	29	0.682	0.691	4.651	0.022
	BT-8	8	0.717	0.729	5.277	0.263
	BT-9	27	0.705	0.725	4.978	0.084
	BT-10	30	0.708	0.669	4.957	0.051
	BT-11	15	0.707	0.733	4.935	0.206
	BT-12	23	0.661	0.633	4.361	0.080
	BT-13	8	0.649	0.622	4.145	0.115
	Mean		0.690	0.686	4.712	0.116
Grande-Terre	GT-1	19	0.735	0.732	4.972	0.065
	GT-2	22	0.705	0.691	4.832	0.085
	GT-3	33	0.728	0.687	5.048	0.205
	GT-4	22	0.684	0.700	4.829	0.124
	GT-5	30	0.681	0.688	4.841	0.123
	GT-6	28	0.722	0.723	5.020	0.110
	GT-7	25	0.720	0.708	4.614	0.075
		Mean		0.711	0.704	4.879

Number of individuals sampled (N), expected heterozygosity (H_E) and observed heterozygosity (H_O), mean standardized allelic richness (A) and mean private standardized allelic richness (PrA) estimated from six individuals are provided for each population.

belonged to one genetic cluster and southern populations from GT belonged to the other cluster, whereas populations from the north (GT1, GT2 and GT3) and from the centre (GT4) of GT presented various levels of admixture between the two previous clusters (Figure 4 and Appendix S2-A). In agreement with such an uppermost level of genetic structure segregating populations from the two parts of the island, 92% of pairwise test of genetic differentiation between populations from BT and GT were significant (after Bonferroni correction, p -values from 0 to <0.001), with pairwise F_{ST} ranging from 0.008 to 0.105 (mean pairwise $F_{ST} = 0.044$, Appendix S3). However, significant and substantial genetic differentiation was also detected between populations within BT and within GT, as 65% (p -values from 0 to <0.001) and 95% (p -values from 0 to <0.001) of pairwise differentiation tests were significant in BT and GT, respectively. Pairwise F_{ST} ranged from 0 to .104 (mean pairwise $F_{ST} = 0.039$) within BT and from 0.009 to 0.056 (mean pairwise $F_{ST} = 0.031$) within GT (Appendix S3). This fine-scale genetic structure within BT and GT was also detected by STRUCTURE as, although weaker, an increase of posterior probability of the data was observed beyond $K = 2$, with up to seven meaningful genetic clusters (Appendix S2-B).

3.3 | Landscape genetics

3.3.1 | Definition of landscape scales and relative performance of resistance surfaces

The optimal spatial extent of the landscape encompassed the sea within the landscape window as this landscape surface (Figure 3e) provided a better AICc value compared to the landscape surfaces wherein the sea was totally (Figure 3a) or partially removed (Figure 3d; Appendix S4). It is worth noting that totally removing the sea from the landscape extent leads to LCP models that performed worse than the model based on Euclidian distances alone (Figure 3a; Appendix S4). Regarding the optimal thematic resolution, the surface describing the sea with two different classes (i.e., coastal sea encompassed in a 1.5-km buffer surrounding the coasts) and open sea (the rest of the sea) provided the LCP model (Figure 3c) with a better support (reduced AICc by 18 units, Appendix S4) compared to the surface describing the sea with a single class (Figure 3b). Surfaces describing agriculture with a single or with three different classes, separating banana and sugar cane plantations from other agricultural areas, lead to equivalent performances of LCP models (Figure 3e,c, respectively; Appendix S4). Therefore, we selected the landscape surface describing agricultural areas with a single class to create a more parsimonious and general model (Figure 3e). The landscape surface resulting from these preliminary tests is presented in Figure 2a and was used in the following analyses.

Resistance surfaces optimized from the three landscape surfaces (elevation, roads, land cover surface including the coastal sea and the open sea and describing agriculture with a single class), independently or in combination, improved the model fit compared to the model based on Euclidian distance alone, regardless of the ecological distance used (Figure 5). In addition, both ecological distances integrating land cover types provided a better explanation of genetic distance compared to ecological distances integrating road network or elevation. It is worth noting that equivalent results were obtained from single surface optimization using an alternative metric of genetic differentiation, G'_{ST} (Hedrick, 2005), which is independent from locus polymorphism (Appendix S5-A). Ecological distance computed from the composite resistance surface did not substantially improve the description of genetic distance compared to the resistance surface based on the land cover alone (Figure 5). Moreover, resistance values of land cover types were unstable across replicates when optimized in combinations with the road and altitude surfaces (multivariate optimization procedure; Appendix S6), whereas they were highly consistent across univariate optimization replicates (See Results "Relative resistance values of the different land cover classes"). Altogether, these results provided a higher support to the resistance surface resulting from the univariate optimization of the land cover surface compared to the composite resistance surface. Therefore, only ecological distances based on the univariate optimization of the land cover surface were considered when comparing the relative performances of IBD, LCP and IBR models.

3.3.2 | Testing relative performances of IBD, LCP and IBR models to explain gene flow

Although significant simple correlation with genetic distance was found for the Euclidian, least-cost and resistance distances, LCP and IBR models based on land cover explained a higher proportion of variance in genetic differentiation than the IBD model (Figure 6). In addition, LCP and IBR models were significantly correlated with genetic differentiation factoring out the influence of Euclidian distance using partial Mantel tests ($r(F_{ST}, \text{resistance}|\text{geographic}) = .53$, $p = .004$; $r(F_{ST}, \text{least cost}|\text{Euclidian}) = .34$, $p = .039$), whereas the IBD model was not significantly associated with genetic differentiation after controlling for each ecological distances ($r(F_{ST}, \text{Euclidian}|\text{resistance}) = .09$, $p = .212$; $r(F_{ST}, \text{Euclidian}|\text{least cost}) = .03$, $p = .416$). Interestingly, the IBR model explained a higher proportion of variance in pairwise genetic distances compared to the LCP model (Figure 6). Causal modelling also supports the IBR over the LCP model, as a significant positive correlation was found between genetic and resistance distances after controlling for least-cost distances ($r(F_{ST}, \text{resistance} | \text{least cost}) = .42$, $p = .017$), whereas no significant correlation was found between genetic and least-cost distances after controlling for resistance distances ($r(F_{ST}, \text{least cost}|\text{resistance}) = -.011$, $p = .472$). It is worth mentioning that results of simple and partial Mantel tests performed in a causal modelling framework and using G'_{ST} lead to the same conclusions (Appendix S5-B), providing an additional support for the IBR over the LCP model.

3.3.3 | Relative resistance values of the different land cover classes

Resistance values optimized for each land cover class were highly consistent among the five replicates (Figure 7). Forest and mangrove and open sea were the most conductive habitat classes, with a slightly higher resistance value for the former. Agriculture and coastal sea were, respectively, about four and seven times more resistant than forest and mangrove. Urban area had the highest resistance value (about 100 times more resistant than forest and mangrove), whereas pasture and inland wetland had intermediate values of resistance to gene flow (Figure 7). These resistance values were qualitatively similar to those obtained from the optimization based on G'_{ST} (Appendix S5-C). In agreement with this vision of the landscape resistance, current density among sampled locations was the highest within the continuous forest on Basse-Terre, whereas the lowest current density was observed across the isthmus, with only a very narrow corridor ensuring connectivity between populations from BT and GT (Figure 7).

4 | DISCUSSION

4.1 | Landscape effects on fine-scale reduction of gene flow in a bird species

A hierarchical genetic structure among sampled locations was found, with populations from Basse-Terre (BT) and from the south

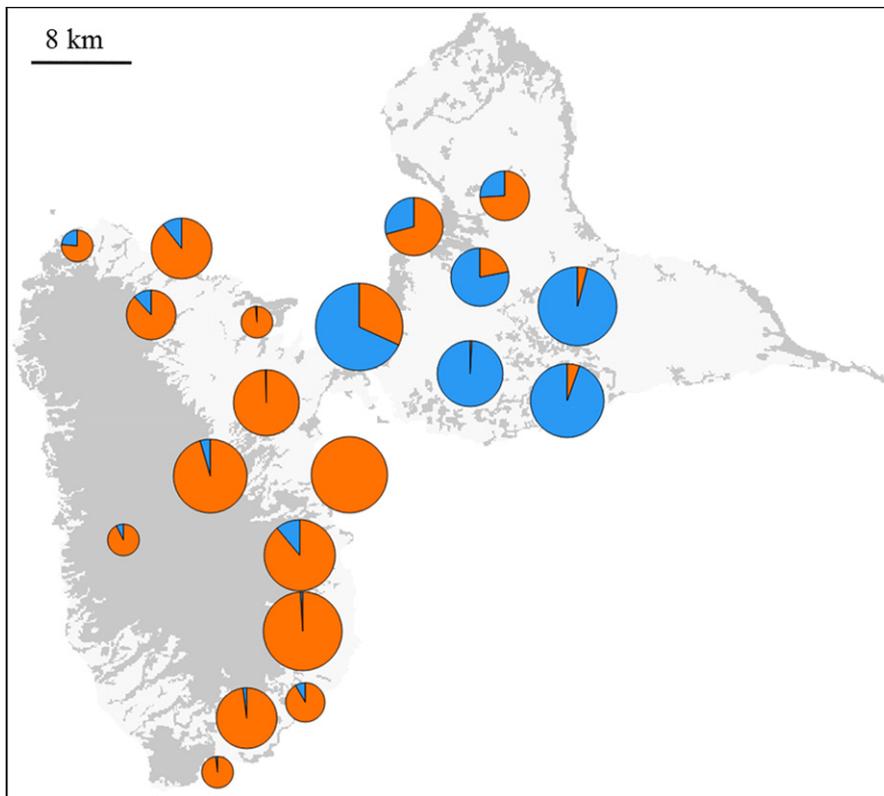


FIGURE 4 Uppermost level of genetic structure detected by STRUCTURE algorithm. The spatial distribution of the forest habitat is depicted in grey. For each population, pie charts represent the membership proportion in the two genetic clusters (in blue and orange). The size of each chart is proportional to sample size [Colour figure can be viewed at wileyonlinelibrary.com]

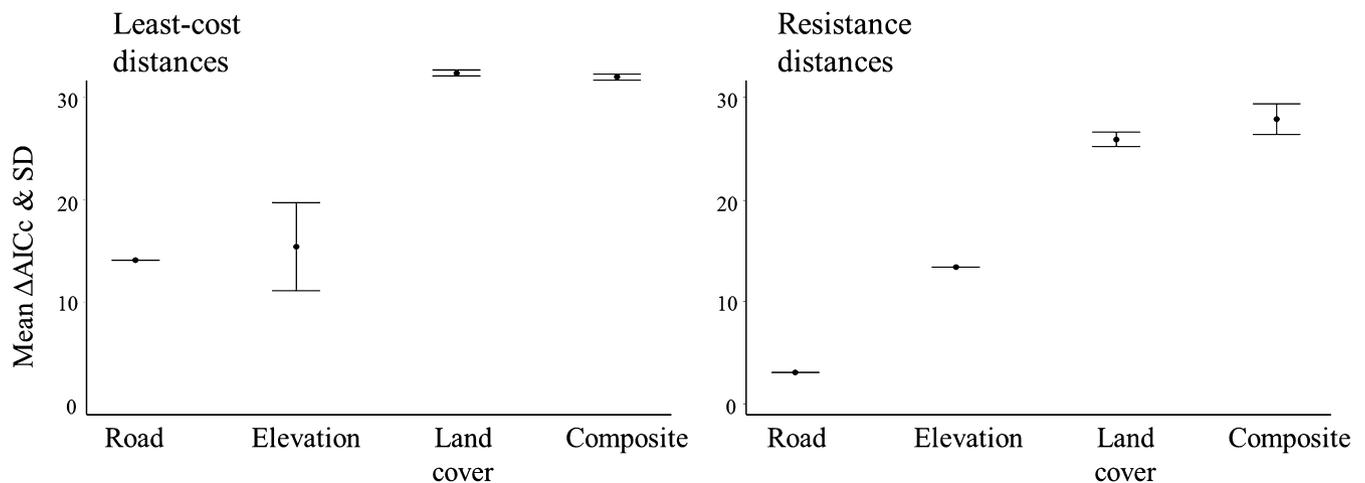


FIGURE 5 Performances of univariate and composite resistance surfaces using least-cost and resistance distances. Univariate optimization of resistance surface was conducted for each of the three landscape surfaces (road, elevation and land cover). In addition, multivariate optimization was also conducted simultaneously for these three landscape surfaces to generate a composite resistance surface (composite). Both univariate and multivariate optimizations used least-cost or resistance distances. Improved performances ($\Delta AICc$) of models based on either least-cost (left panel) or resistance (right panel) distances compared to the model based on Euclidian distances were averaged across the five replicates (mean $\Delta AICc$) and standard deviations (SD) are depicted

of Grande-Terre (GT) mainly segregated into two genetic entities. In addition, further genetic structure was found at a finer spatial scale within BT and GT. Evidences of small-scale reduction of gene flow are starting to accumulate in birds (Arnoux et al., 2014; Bertrand et al., 2014; Callens et al., 2011; Khimoun, Arnoux, et al., 2016; Khimoun, Eraud, et al., 2016), demonstrating a contrast between intrinsic dispersal abilities and realized dispersal in these organisms. Here, this fine-scale genetic structure is driven by ecological factors

as attested by results of the causal modelling, which rejects the hypothesis of isolation by distance. Indeed, a significant positive correlation was found between ecological and genetic distances after controlling for Euclidian distance, but the converse was not found.

Land cover type was a prominent factor affecting gene flow in the Plumbeous Warbler, with elevation and roads having a negligible effect (Figure 5). Although elevation may act as a barrier to gene

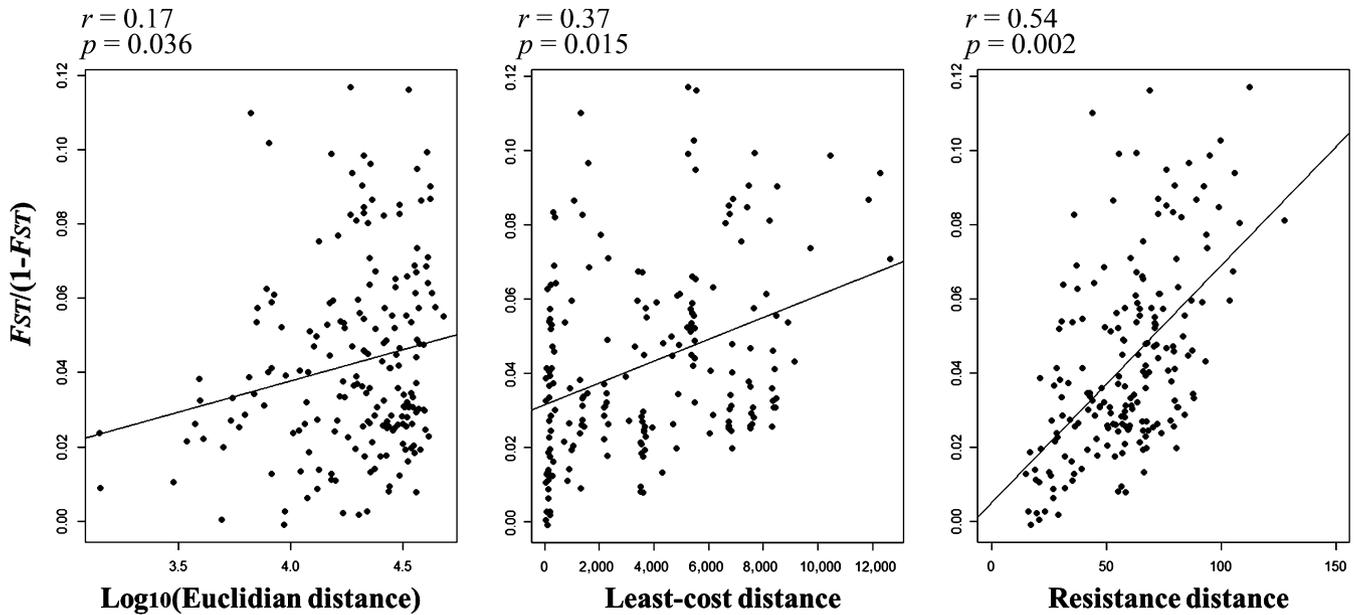


FIGURE 6 Results of simple Mantel correlation tests between genetic differentiation and Euclidian or ecological distances between pairs of populations. Least-cost and resistance distances were calculated from the optimized resistance surface relying on the land cover surface defined in the preliminary analyses. Spearman correlation coefficients (r) between pairwise genetic distances ($F_{ST}/(1 - F_{ST})$) and Euclidian, least-cost or resistance distances are provided

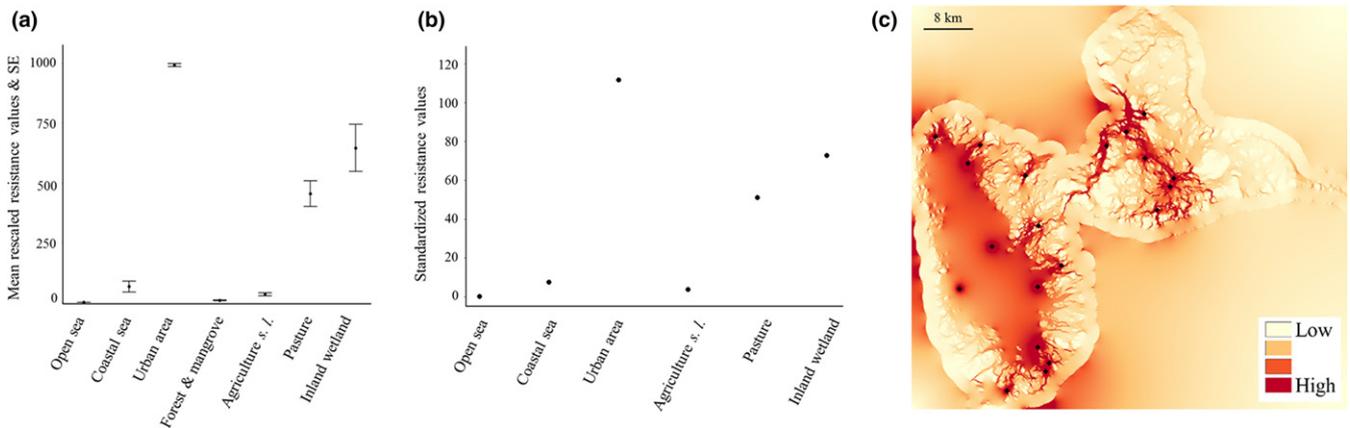


FIGURE 7 Optimized land cover resistance values and current flow density between sampled populations. (a) For each land cover class, rescaled resistance value averaged across the five replicates and standard error (SE) are provided. (b) Standardized resistance values were obtained for each land cover class by dividing the resistance of the land cover classes by the resistance value of forest and mangrove. (c) According to the optimized resistance values, current flow density is represented between sampled populations on the right panel [Colour figure can be viewed at wileyonlinelibrary.com]

flow in some bird species (Adams, Lazerte, Otter, & Burg, 2016; Caizergues et al., 2003), such an effect was not detected here, probably because the elevation in Guadeloupe does not exceed 1,500 m and because the highest elevations are located in the westernmost part of the island. We also detected a relatively negligible effect of roads compared to land cover, although roads constitute a prominent barrier to gene flow in many organisms (e.g., ground beetles, Keller and Largiadèr (2003); bighorn sheep, Epps et al. (2005)). Bird species may also exhibit reluctance to cross roads that are 10–30 m wide (Develey & Stouffer, 2001). Nonetheless, the behavioural barriers caused by roads may be related to the width of the gap they

create in the surrounding habitat (Kociolek, Clevenger, St Clair, & Proppe, 2011), and this effect may be accurately captured by land cover.

4.2 | Differential effects of matrix components on gene flow: insights into dispersal in fragmented landscapes

Water commonly acts as a strong behavioural barrier to terrestrial bird movement (Harris & Reed, 2002). However, open sea and coastal sea appear to have a relatively low resistance to gene flow

in this study. The compulsory nature of oversea movements, once they have been initiated, may explain this apparent contradiction. In addition, dispersal behaviour may be modified in response to dispersal-related costs (e.g., loss of energy and mortality) induced by habitat fragmentation (Knowlton & Graham, 2010). Behavioural response to costs and risks of dispersal in modified landscapes may affect the first stage of dispersal (i.e., emigration decision), as animals may be reluctant to cross habitat boundaries in fragmented landscapes (Bélisle & Desrochers, 2002; Desrochers, Bélisle, Morand-Ferron, & Bourque, 2011; St-Louis et al., 2014). The higher resistance of coastal sea compared to the open sea could reflect such a reluctance to cross the land–sea ecotone. Behavioural adaptations to reduce the cost of dispersal in fragmented landscape may also affect the second step of dispersal (i.e., travelling through a more or less inhospitable matrix). Indeed, in fragmented landscapes, animals have straighter (and thus shorter) movement within inhospitable matrix, whereas less directional movements within suitable habitat lead to more tortuous pathways (Goodwing & Fahrig, 2002; Prevedello, Forero-Medina, & Vieira, 2010; Schtickzelle, Joiris, Van Dyck, & Baguette, 2007). Here, the slightly higher resistance of the forest and mangrove compared to the open sea could be explained by such differences in dispersal behaviour within and outside the forest habitat. Indeed, within-habitat dispersal resulting from routine and exploratory movements (i.e., foraging, prospecting for mate or nesting site) can result in a high level of returning and low level of net displacement (Van Dyck & Baguette, 2005), which consequently can lead to greater resistance to movement within the forest and mangrove habitat. On the other hand, overwater dispersal outside the forest habitat could result from a special type of movement, more directed and associated with high level of net displacement (Van Dyck & Baguette, 2005), leading to a lower cost to disperse over the open water.

Regarding relative resistances of the different land cover classes, all nonforest land cover types negatively impact the landscape functional connectivity, as they were from four (for agricultural area) to 100 (for urban area) times more resistant to gene flow than forest and mangrove. Relative resistance values of nonforest habitat are consistent with the general finding that matrix quality increases with increasing structural similarity with habitat patches (Prevedello & Vieira, 2009). Indeed, urban and open areas (meadows) have the highest resistance values, whereas agricultural area, which is intermediate in terms of vegetation structure compared to forest/mangrove and meadows, had an intermediate resistance value. Previous studies on forest bird movement (e.g., travel trajectories, homing return time or success) in heterogeneous landscapes reported their reluctance to cross open areas such as agricultural fields or pastures, preferring to move along forest edges even when resulting in longer travel times (Bélisle & Desrochers, 2002; Bélisle, Desrochers, & Fortin, 2001; Desrochers et al., 2011; St-Louis et al., 2014). Altogether, these results highlighted the relevance of the optimization approach developed by Peterman et al. (2014) to explicitly test hypotheses concerning the relative role of

matrix components on gene flow. It also allows detection of potentially important corridors as shown by current density for the Plumbeous Warbler in the urbanized isthmus connecting BT and GT.

4.3 | Resistance distance outperformance: implication for connectivity conservation

Causal modelling supported the IBR model in the Plumbeous Warbler, as resistance distances relying on circuit theory outperformed least-cost distances to predict patterns of genetic differentiation. Previous empirical studies comparing relative performances of LCP and IBR models have reported conflicting results (Moore, Robinson, Lovette, & Robinson, 2008; Schwartz et al., 2009; Trumbo, Spear, Baumsteiger, & Storer, 2013). The match between the underlying assumptions of each model and biological characteristics of the studied species may explain such mixed results. Here, the superior performance of IBR over LCP emphasizes the importance of integrating multiple alternative pathways instead of considering a single optimal pathway when describing the dispersal behaviour of the Plumbeous Warbler within the fragmented landscape of the Guadeloupe Island. Such nonoptimal animal movements in human-modified landscapes challenge the underlying assumptions of LCP modelling (Fahrig, 2007). Despite increasing applications of modelling resistance across multiple pathways (e.g., CIRCUITSCAPE; McRae, 2012), LCP is the most widely used criteria to design habitat corridors in the growing field of connectivity conservation (La Rue & Nielsen, 2008; Marrotte & Bowman, 2017; Sawyer, Epps, & Brashares, 2011). Our results advocate for a broader use of models using multiple pathways in linkage-design methodology, as this alternative approach may provide more reliable model outputs for conservation. They also highlight the importance, in some species, of protecting/restoring multiple pathways for dispersal in human-altered landscapes, although practitioners usually have to make prioritization decisions because of several constraints (e.g., social, economic and legal).

4.4 | On the usefulness of resistance surface optimization to objectively define landscape scales

Preliminary analyses highlighted the importance of identifying the appropriate spatial extent and thematic resolution of the landscape. Alternative classification schemes of habitat types in the land cover surface provided the corresponding optimized resistance surface with heterogeneous ability to predict genetic differentiation. More importantly, misspecification of the landscape extent may have serious consequences for landscape genetics inferences. Indeed, the exclusion of sea pixels from the land cover classification led to lower performance of models based on ecological distances compared to models based on Euclidian distances only. Exclusion of sea pixels would have led to the erroneous conclusion of the absence of landscape effect on gene flow. The increasingly popular approach of resistance surface parameterization based on species distribution models (Wang, Yang, Bridgman, & Lin, 2008) or resource selection

functions (Boyce, Vernier, Nielsen, & Schmiegelow, 2002; Shafer et al., 2012) would restrict the landscape extent to terrestrial land surfaces only. Our results illustrated the potential pitfalls associated with the parameterization of resistance surfaces based on biological or ecological models describing processes that are not related to the movement of genes across the landscape. These results support previous theoretic and empirical evidences of scale dependencies in individual-based landscape genetic inferences (Cushman & Landguth, 2010a; Wasserman, Cushman, Schwartz, & Wallin, 2010). Consequently, our results emphasize the need for a preliminary exploration of landscape-scale dependencies (i.e., landscape extent and thematic resolution) in landscape genetics studies and suggest that our two-step implementation of the optimization procedure developed by Peterman et al. (2014) can be a useful and operational approach to objectively define the appropriate landscape scales.

5 | CONCLUSION

This work is one of the rare landscape genetics studies conducted in the tropics. Although birds may be considered as not much sensitive to anthropogenic disturbance given their high intrinsic dispersal abilities, our results highlight the negative effects of forest fragmentation on a forest specialist avian species and suggest that consequences of habitat fragmentation and loss may have been underestimated in a priori mobile organisms, especially in tropical regions. In addition, this work provides an important contribution in landscape genetics methodology by providing a framework to quantitatively assess the influence of alternative scales or landscape definitions and to accurately define the landscape scales, an important but often overlooked issue in empirical studies. This study proposes a step-by-step procedure for conducting landscape genetics analyses without a priori specific knowledge about dispersal, which may be particularly relevant for assessing population connectivity in nonmodel and/or understudied species, but also for testing resistance estimations commonly based on habitat suitability maps or expert opinion.

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DATA ACCESSIBILITY

Microsatellite genotyping: <https://doi.org/10.5061/dryad.v8324>.

AUTHOR CONTRIBUTIONS

S.G., B.F. and C.E. designed the study and obtained the funding; S.G. and C.E. managed fieldwork performed by S.G., B.F. and many other collaborators; A.K. performed laboratory work; A.K. analysed data with contributions of S.G., N.N. and W.P.; A.K. and S.G. wrote the manuscript with the contribution of all co-authors.

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