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Genetic costructure in a meta-community under threat of habitat fragmentation

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Abstract

Habitat fragmentation increasingly threatens the services provided by natural communities and ecosystem worldwide. An understanding of the eco-evolutionary processes underlying fragmentation-compromised communities in natural settings is lacking, yet critical to realistic and sustainable conservation. Through integrating the multivariate genetic, biotic and abiotic facets of a natural community module experiencing various degrees of habitat fragmentation, we provide unique insights into the processes underlying community functioning in real, natural conditions. The focal community module comprises a parasitic butterfly of conservation concern and its two obligatory host species, a plant and an ant. We show that both historical dispersal and ongoing habitat fragmentation shape population genetic diversity of the butterfly *Phengaris alcon* and its most limited host species (the plant *Gentiana pneumonanthe*). Genetic structure of each species was strongly driven by geographical structure, altitude and landscape connectivity. Strikingly, however, was the strong degree of genetic costructure among the three species that could not be explained by the spatial variables under study. This finding suggests that factors other than spatial configuration, including co-evolutionary dynamics and shared dispersal pathways, cause parallel genetic structure among interacting species. While the exact contribution of co-evolution and shared dispersal routes on the genetic variation within and among communities deserves further attention, our findings demonstrate a considerable degree of genetic parallelism in natural meta-communities. The significant effect of landscape connectivity on the genetic diversity and structure of the butterfly also suggests that habitat fragmentation may threaten the functioning of the community module on the long run.

KEYWORDS
co-evolution, connectivity, costructure, dispersal, Gentiana pneumonanthe, *Phengaris alcon*

1 | INTRODUCTION

Biotic interaction networks including pollination, competition and parasitism play a key role in community functioning and persistence, but global environmental changes compromise their ecological and evolutionary stability (Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010; Strona & Lafferty, 2016; Tylianakis, Didham, Bascompte, & Wardle, 2008). Fuelled by ongoing land conversions, habitat fragmentation in particular increasingly degrades ecological communities and ecosystems across the globe (Haddad et al., 2015; Newbold et al., 2015). Yet attempts to mitigate these impacts are hampered by a markedly poor understanding of the eco-evolutionary dynamics driving biotic interaction networks under threat of habitat fragmentation (Legrand et al., 2017; Titeux, Henle, Mihoub, & Brotons, 2016; Toju et al., 2017). Indeed, owing to technical challenges associated with studying eco-evolutionary community processes in natural settings, nonexperimental empirical studies demonstrating how biotic interactions implicate the ability of species to withstand habitat fragmentation are lacking.

Theoretical models and experimental work on microbial communities predict that habitat fragmentation and community functioning are linked through the effects of landscape connectivity on dispersal, the latter defining individual movements across the landscape (Staddon, Lindo, Crittenden, Gilbert, & Gonzalez, 2010; Thompson, Rayfield, & Gonzalez, 2017; Urban et al., 2008; Venail et al., 2008). According to these in silico and in vitro studies, intermediate levels of dispersal facilitate community dynamics, whereas low (or high) levels of dispersal can deplete (or swamp) locally adapted communities. However, the processes determining eco-evolutionary outcomes are highly variable, shaped by species' genetic architecture, their phenotypic variation, the strength and amount of interactions with local biotic and abiotic variables, and the eco-evolutionary feedbacks resulting from interactions between each of these components (Baguette, Blanchet, Legrand, Stevens, & Turlure, 2013; Legrand et al., 2017). This complexity is compromising empirical validation of theoretical predictions, urging for a more realistic perspective on the impacts of altered landscape connectivity on communities and ecosystems (Cote et al., 2017; Kokko et al., 2017; Logue, Mouquet, Peter, & Hillebrand, 2011).

Analogous to the interwoven nature of community dynamics and adaptive evolution, we propose the integration of landscape genetic disciplines in community ecology (Hand, Lowe, Kovach, Muhlfeld, & Luikart, 2015) to address this complexity in situ. Ecological and evolutionary processes including drift, gene flow, and abiotic and co-evolutionary selection directly influence patterns of genetic variation within and among communities. Co-evolution in particular may give rise to distinct genetic signatures when communities are spatially structured. More specifically, spatial community structure can generate a geographic mosaic of co-evolutionary hot spots featured by strong reciprocal selection among interacting species (Nuismer, Thompson, & Gomulkiewicz, 2000; Thompson & Cunningham, 2002; Thrall et al., 2012). Where local co-evolution prevents successful immigration of maladapted (nonlocal) individuals, or when it favours reduced dispersal ability in isolated habitats (Start & Gilbert, 2016), such selection mosaics can result in paralleled genetic structure among interacting species (Räsänen & Hendry, 2008). In addition to co-evolution, similar geneflow patterns among interacting species may cause genetic overlapping patterns in genetic structure. Assessing population genetic variation within and among the different species of a community network may therefore shed light on the impact of habitat fragmentation on community dynamics.

Here, we study the impacts of habitat fragmentation on the genetic variation within and among interacting species in natural settings. We focus on a community system highly appreciated for its conservation value: the threatened and specialized European butterfly *Phengaris (=Maculinea) alcon alcon* (the Alcon blue) and its two obligatory hosts, a rare grassland plant *Gentiana pneumonanthe* (the marsh gentian) and an ant of the genus *Myrmica* (here the widespread *Myrmica scabrinodis*) (Figure 1a) (Nash, Als, Maile, Jones, & Boomsma, 2008; Valdés & Ehrlén, 2017;). Due to habitat fragmentation, the butterfly faces local extinctions across its range, even where its hosts remain locally abundant (Mouquet et al., 2005). This meta-community is also featured by specialized co-evolutionary mechanisms (e.g., synchronized phenology and physiology, Nash et al., 2008; Valdés & Ehrlén, 2017). We focus on a mountainous landscape in the French department Ariège (4,890 km^2), where we investigated all known Alcon communities. These community sites are spatially structured into four disjoint clusters (meta-communities), with among-cluster distances (>10 km) exceeding the known maximum dispersal distance of the butterfly (0.5 km) (Figures 1b-d, S1).

The key questions of this study are as follows: (i) Does population genetic diversity of the parasitic Alcon and its two host species decrease with increasing levels of habitat fragmentation? (ii) To what extent does population genetic structure coincide between the parasitic Alcon and its two host species? And (iii) which factors drive the amount of genetic co-variation between the three species?

2 | MATERIAL AND METHODS

2.1 | Study system

The Alcon blue (*Phengaris* [=*Maculinea*] *alcon*) is a rare Eurasian butterfly with a unique lifestyle involving obligatory parasitism on two successive host species: the marsh gentian plant (*Gentiana pneumonanthe*) and an ant species of the genus *Myrmica* (Mouquet et al., 2005; Nash et al., 2008). After mating, female Alcon blue butterflies lay their white eggs onto gentian flower buds. Small caterpillars develop into the bud, at the expense of gentian's ovules. This host–parasite interaction has been shown to result in co-evolutionary shifts in flower phenology to escape peak Alcon infestations (Valdés & Ehrlén, 2017). After their third moult, the caterpillars leave the plant and are adopted by *Myrmica* ants, which recognize the chemical signature of the caterpillars as their own. The ants subsequently rear them into their underground nest in preference to their own brood. This social parasitism has been demonstrated to give rise to co-evolutionary changes in surface chemistry of Myrmica and Alcon larvae (Nash et al., 2008).

Ongoing increases in forest cover across the Pyrenees threaten the existence of numerous grassland species and communities, including this highly appreciated butterfly and its host plant (Galop, Rius, Cugny, & Mazier, 2013; Metailié & Paegelow, 2005). The butterfly in particular is suffering strong declines across the Pyrenees, as increased habitat fragmentation leaves most viable plant populations (>50 flowering individuals) without butterflies (Tessier, 2015). In the Pyrenees, the plant is typically associated with moist grazed grassland where the limestone-based and clay-rich soil (e.g., marl) is

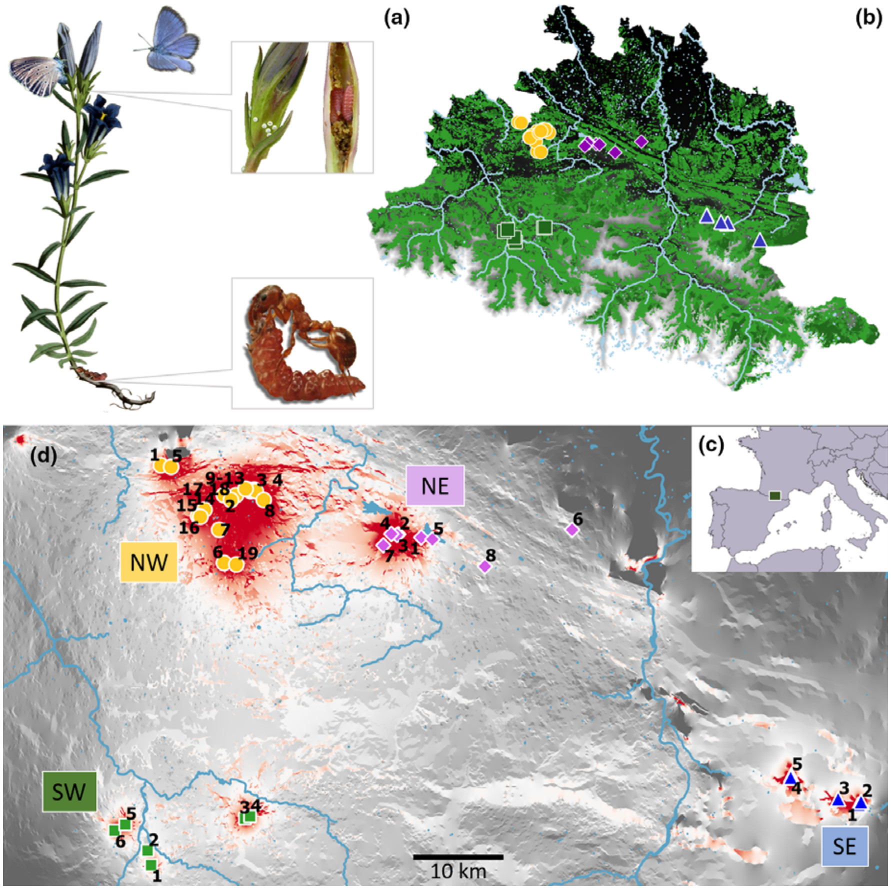

FIGURE 1 Study system. (a) Butterfly community module. For visibility, ant size was exaggerated relative to plant size. (b) Overview of the study landscape in which the samples were collected, with tree cover shown in green, and with a black to white gradient reflecting altitude. Shape and colour of sampling locations correspond to their geographical cluster (yellow circles: NW, purple diamonds: NE, blue triangles: SE, green squares: SW). (c) Positioning of sampling area in the French central Pyrenees (SW Europe). (d) Landscape connectivity map of the study area representing butterfly dispersal probability. Red colours represent habitat favouring dispersal (i.e., low landscape resistance or high landscape connectivity). Grey colours represent habitat impeding dispersal. Rivers (blue) align with the main valleys. Geographical and demographic details about the sampling sites can be found in Table S1 [Colour figure can be viewed at wileyonlinelibrary.com]

locally decalcified due to the accumulation of rain water (Tessier, 2015). Cattle and large herbivores are assumed to allow regular seed dispersal among sites occupied by the plants through the transport of seed-containing mud. At these sites, the nests of the host ant, *Myrmica scabrinodis*, to our knowledge the principal and widespread ant host of the butterfly in the Pyrenees, are found on the drier parts, where the soil is locally more permeable. In the department of Ariège in the central French Pyrenees, butterfly sites are present in four spatially separated regions (Figure 1). This spatial structuring is consistent with relatively localized dispersal events observed during daily capture–mark–recapture (CMR) monitoring at 17 sites, showing some dispersal within geographical clusters (3.55% butterflies recaptured in another site vs. 35.49% recaptured on site), limited dispersal among the nearest clusters (0.51%) and no dispersal among the more distant clusters (Figure S1).

2.2 | Sampling and genotyping

Phengaris alcon (Lycaenidae, hereafter "Alcon") and its two hosts, *G. pneumonanthe* (Gentianaceae, hereafter "Gentian") and *M. scabrinodis* (Formicidae, hereafter "Myrmica"), were sampled for genetic material across the four butterfly-occupied clusters in the Ariège department during the summers of 2014 and 2015 (Figure 1). A leg from each of 915 butterflies (27 sites), collected during the CMR monitoring, as well as 843 ants (32 sites), baited on 5-metre grids across the sites and individually identified using a microscope, and leaves from 1159 plants (37 sites), were processed for DNA using DNeasy extraction kits (Qiagen Inc., Valencia, CA, USA). Based on flowering plant counts at 15 sites, we know that larger habitat sizes contain more reproductive host plants ($r = .80$, $p < .0001$ after log10 transformation). The communities span an altitudinal gradient from 400 to 1,017 m, with patch sizes varying between 275 and 17,359 m^2 (Table S1).

Pooled, paired-end restriction-associated DNA (RAD-PE) sequencing was used to obtain allele frequency (AF) estimates from the DNA samples of each species (Appendix S1). For the butterfly, the plant and the ant, read assembly and SNP calling (Appendix S1) generated a total of 2,413, 2,205 and 2,414 SNPs with a mean coverage of 64 (±42), 35 (±14) and 94 (±61), and with 42%, 62% and 50% missing data, respectively. SNPs and pools with missing AF data and a minimum coverage <20 were removed from the data set, finally resulting in 478 (Alcon, 22 populations), 184 (Gentian, 37 populations) and 166 bi-allelic SNPs (Myrmica, 29 populations), with a mean coverage of 128 (±27), 65 (±29) and 197 (±66), respectively (Figure S3d). The limited number of SNPs together with the choice of retaining maximum 1 SNP per RAD-tag minimizes physical linkage among SNPs. Where pool replicates were available, the mean AF was used. To assess the reliability of the AF estimates, AFs were compared between duplicate pools (Figure S3a–c). The SNPs are assumed to be randomly distributed across the genome and to predominantly reflect neutral genetic processes.

2.3 | Modelling of habitat fragmentation

Based on the assumption that butterfly movement and persistence are mainly affected by habitat type and host plant distribution, landscape resistance was calculated between each pair of sites using a land cover map, a map of the 164 known plant sites in Ariège, and the potential presence of the host plant based on a geological map. Geology was included because it has been found to be strongly associated with the presence of Gentian plants (Tessier, 2015). A total of five dispersal cost values were assigned to the different land cover types, with higher dispersal costs assigned to habitat features that likely increase dispersal resistance throughout the landscape (Table S2). For example, high dispersal cost values were assigned to forests relative to grasslands corresponding to the lack of food and host plant resources discouraging movement into forests and in line with field observations. The host plant and geology map each consisted of two cost categories indicating (likely) absence vs. (likely) presence of host plants. To test different relationships between landscape features and gene flow, a total of 40 dispersal cost surfaces were built at a resolution of 30 m using QGIS 2.14, based on the original cost categories as well as on polynomial cost functions (x^2, x^3 and x^4) representing various magnitudes of dispersal costs. For each cost surface, landscape resistance was calculated between all pairs of sites using an eight-neighbour-cell regime in CIRCUITSCAPE (McRae, Dickson, Roemer, & Rundall, 2013).

Aiming to select the most appropriate cost surface for further analysis, the relative contribution of geographical distance and landscape resistance to the genetic distance among Alcon populations was calculated by means of partial Mantel correlation tests (Mantel, 1967; Smouse, Long, & Sokal, 1986), using the R package "Vegan" (Oksanen et al., 2008). More specifically, the relationship between the genetic and the geographic matrix was evaluated while holding the landscape resistance matrix constant. Conversely, the relationship between the genetic and landscape resistance matrix was evaluated while controlling for the geographical matrix. The genetic distance (F_{ST}) matrix was calculated using the R package "ade4" (Dray, Dufour, Thioulouse, Jombart, & Pavoine, 2009), based on the Alcon allele frequency matrix. The cost surface best explaining the among-population genetic distances was used as a proxy for the effective amount of dispersal. High landscape resistance thus corresponds to low landscape connectivity, or high levels of Alcon habitat fragmentation, resulting in increased genetic differentiation among populations.

As F_{ST} is known to be sensitive to the influence of effective population sizes (i.e., genetic drift), we conducted multiple regression on distance matrices (MRDM; Smouse et al., 1986). The F_{ST} matrix was used as the dependent variable, while two metrics designed to capture the unique influence of spatial heterogeneity in local drift on genetic differentiation (or spatial heterogeneity in effective population sizes (SHNe); Prunier, Dubut, Chikhi, & Blanchet, 2017) were included as predictors. We considered the two possible metrics dhm (distance based on the harmonic mean of census population sizes) and di (distance based on the inverse of heterozygosities) (see Prunier et al., 2017; Table S3). Both metrics were calculated from local patch sizes as a proxy for census population size.

2.4 | Statistical modelling of genetic diversity

Genetic diversity HE (expected heterozygosity, Box 1) (Nei, Maruyama, & Chakraborty, 1975) was calculated for each population and each species as 2AF(1-AF), averaged across loci (Figure S4). Expected heterozygosity is insensitive to rare alleles and therefore provides conservative estimates of recent demographic population changes (Luikart & Cornuet, 1998; Nei et al., 1975).

For each species, a weighted linear regression model was used to uncover the relative contribution of altitude, habitat size (log10-transformed) and landscape resistance (Alcon) or geographical isolation (host species) on population genetic diversity, with higher residual weights for larger pools. Habitat size was used as an integrative approximation of population size because (i) Alcon butterfly population sizes greatly fluctuate from year to year and (ii) butterfly counts (Figures S1, S5) did not alter model outcomes as compared to habitat size (Table S4). Landscape resistance (Box 1) was calculated as the mean pairwise landscape resistance among the focal site and all other sites based on the selected cost surface obtained through CIRCUITSCAPE, with the reasonable assumption of no Alcon sites outside the study area contributing to dispersal into the study area. Geographic isolation of the host populations was calculated as the average pairwise distance to the five nearest known communities. Variance inflation factors (VIFs) and pairwise Pearson's correlation coefficients were provided to assess variable multicollinearity for each species (Table S5). The variables described in the models above

BOX 1 Terminology

Community module: A spatial network of a confined number of interacting species (here a butterfly, a plant and an ant species).

Genetic diversity: Within-population variation at genetic markers (here single-nucleotide polymorphism loci) averaged across loci.

Landscape resistance: The degree to which landscape characteristics impede butterfly movement (dispersal) and persistence across the landscape. Landscape resistance was estimated for each pair of butterfly sites and then averaged across all pairs per site to obtain a measure of landscape resistance for each site. Landscape resistance is the inverse of landscape connectivity and reflects the degree of butterfly habitat fragmentation resulting in increased genetic differentiation among populations.

Genetic parallelism: The degree of co-variation between butterfly and host genetic structure (also genetic costructure or genetic co-variation).

had VIFs varying between 1.02 and 2.19, that is below the commonly applied threshold of 5 (Zuur, Ieno, & Elphick, 2010).

Community-level patterns of diversity, that is co-varying genetic diversity patterns among Alcon and its two host species, were examined through regressing Alcon HE ~ Gentian HE + Myrmica HE, using the 19 populations for which allele frequency (AF) estimates for each of the three species were available (Table S1).

Because high parasitic butterfly densities are expected to impact host abundance and HE, we tested for potential negative effects of local Alcon density on host HE. Alcon density was estimated based on the number of captures in a site (see Figure S1) divided by habitat size (Table S1). The ten sites that were not part of daily screenings were visited during the peak of the flying season, and number of captures of the best day (most captures, which correlated with total number of captures during the flying season, Figure S1) was used as a proxy for parasitic impact (Turlure, Pe'er, Baguette, & Schtickzelle, 2017). Because Alcon density counts may be sensitive to yearly fluctuations, the results will be discussed in view of genetic diversity relations between Alcon and its hosts.

2.5 | Statistical modelling of genetic structure

To assess the role of landscape resistance (for Alcon), geographical isolation (for host species), geographical position, altitude and patch size as potential drivers of genetic structure, multivariate genetic analyses were performed between the genetic structure of each species and environmental variables using redundancy analysis. More specifically, the Hellinger-transformed allele frequency (AF) matrix of each species was modelled as a multivariate response to latitude, longitude, altitude, habitat size and landscape resistance (for Alcon) or geographical isolation (for host species) as explanatory variables, using canonical redundancy analyses (RDAs). To reduce the strong correlation between spatial (latitude and longitude) and other variables, the geographical coordinates were rotated by 10°. This allowed partial uncoupling of spatial from remaining variables, consequently reducing multicollinearity among variables while respecting the relative position of each population (Table S5). We applied forward selection with a *p*-value threshold <0.1 for variable selection as implemented in the R package *Packfor* (Legendre & Legendre, 1998; Oksanen et al., 2008). Variation partitioning was used to extract the unique contributions of each variable to the genetic structure while accounting for common effects among the variables, using the R package *Vegan* (Figure S6). Significance of unique fractions was tested by permutation tests (9,999 randomizations). This was carried out in *Vegan* using partial redundancy analyses, which test the contribution of a variable while removing the effect of constraining variables (Oksanen et al., 2008).

2.6 | Statistical modelling of genetic costructure

To identify the degree of co-variation between Alcon and host genetic structure (i.e., costructure), a co-inertia analysis was performed between the Hellinger-transformed AF matrix of the Alcon on the one hand, and the Hellinger-transformed AF matrices of the hosts (R package ade4) (Dray et al., 2009). The RV-coefficient, representing the strength of the co-variation, was calculated and statistically tested using Monte Carlo permutation tests (9,999 permutations). To assess the effect of spatial variables (latitude, longitude, altitude) and habitat fragmentation (resistance) on the degree of co-variation between butterfly and host genetic structure, the co-inertia scores extracted from the co-inertia analysis were used as response variables in a RDA with latitude, longitude, altitude and resistance as explanatory variables.

3 | RESULTS

3.1 | Landscape resistance between butterfly patches

Strong isolation by distance was observed for all cost surfaces, with partial Mantel correlations ranging from $r = .520$ to $r = .541$ ($p < .005$, Table S6). In addition to geographical distance, inhospitable landscape features did not contribute to the genetic distance among butterfly populations through increasing landscape resistance ($r = .0674$–.105, $p > .05$, Table S6). The cost surface composed of geology^1, gentian presence^1 and land cover^2 rendered the highest partial Mantel correlation ($r_{\text{total}} = .628$, $r_{\text{geo}} = .525$, $r_{\text{resistance}} = .103$, Figure 1d). With exception of geographical distance, land cover therefore is the most important determinant of genetic connectivity across the landscape. On average, site SE2 is most isolated from all other sites, as indicated by a mean pairwise landscape resistance of 21.33, which is in line with CMR monitoring providing only one immigrant observation (Figure S1). Site NW17, on the other hand, is most connected based on a mean pairwise landscape resistance of 11.44 and on the observation of regular immigration (Figure S1).

Although di showed a slightly higher contribution to the variance in F_{ST} than dhm (Udi = 0.01/Udhm = 0.05), 95% confidence intervals around beta weights included 0 in both metrics, indicating that F_{ST} values were not impacted by SHNe in our system (Table S3). We therefore assume that the relations between genetic distance and landscape resistance observed here are not affected by heterogeneity in effective population sizes.

3.2 | Community genetic diversity

Highest HE was observed for the Gentian (0.33 ± 0.01), followed by the Alcon (0.23 ± 0.02) and Myrmica (0.14 ± 0.01). Alcon HE decreased significantly with increasing landscape resistance ($p < .01$, Figure 2a) and with altitude ($p < .05$, Figure 2b), both factors explaining a total of 74.23% of variation in HE ($F_{3,18} = 21.04$). Altitude also was a significant explanatory variable of Gentian HE ($R^2 = .46$, $F_{2,34} = 9.34$, $p < .001$, Figure 2b), as opposed to Myrmica HE ($R^2 = .06$, $F_{2,26} = 0.89$, $p > .05$, Figure 2b). Whereas HE decreased with increasing altitude, field observations for 15 populations indicate no decline in census population size with altitude for both the butterfly and the plant (Figure S5). Neither patch area nor

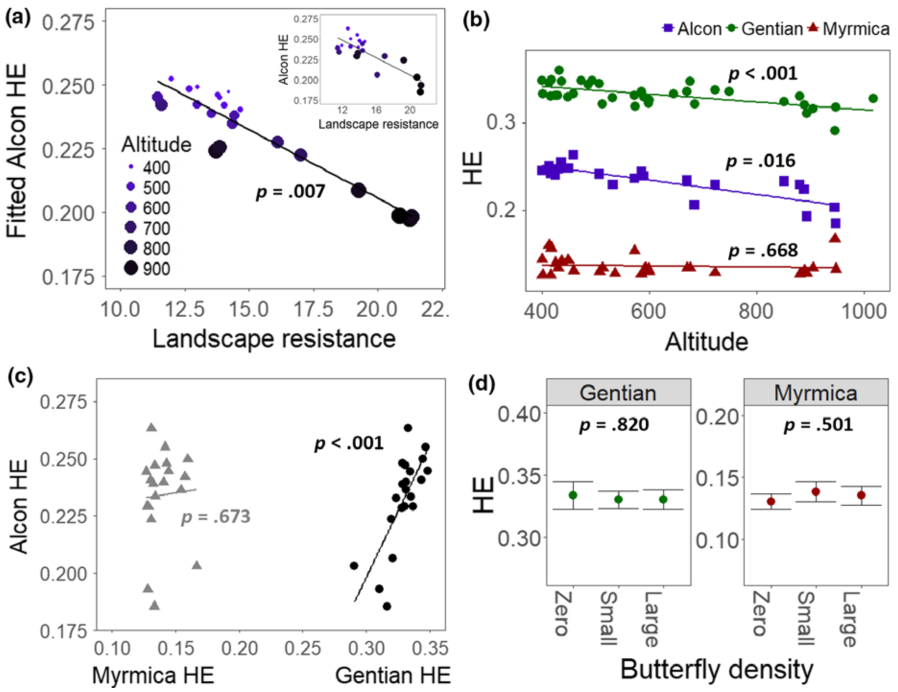

FIGURE 2 Genetic diversity (HE) patterns of the butterfly community module. (a) Correlation between landscape connectivity and fitted and original butterfly H_E values. Fitted values result from a weighted linear model with landscape resistance, altitude and patch size (log10-transformed) as explanatory variables (Table S4). Dots get darker and larger with altitude. (b) Correlation between altitude and genetic diversity of each species. (c) Relation between butterfly and host genetic diversity for both high landscape connectivity (>7.2, the median) and low landscape connectivity (<7.2). (d) Parasitic effect of the butterfly (based on local population densities) on genetic diversity of hosts. Zero butterfly density refers to recently extinct populations [Colour figure can be viewed at wileyonlinelibrary.com]

geographical isolation explained HE patterns in any of the species (Table S4). Weighing the model residuals by pool size had a negligible effect on regression outcomes (Table S4).

Regression modelling revealed a significant positive association between Alcon HE and Gentian HE ($p < .001$), but not between Alcon and Myrmica HE ($p > .05$, Figure 2c, Table S4). Host HE was not affected by local Alcon density, indicating no apparent parasitic impact of Alcon on genetic diversity of its hosts (Figure 2d).

3.3 | Community genetic structure

The proportion of the among-population genetic variation that could be explained by the variables retained by the RDAs was 20.91%, 36.03% and 13.72% for Alcon, Gentian and Myrmica, respectively (Table S4). Altitude significantly affected the genetic structure of all species (Figure 3a–c, Table S4), even after accounting for all co-variables (Figure 4). Only Gentian genetic structure was strongly determined by the geographical position of the populations, as demonstrated by the unique and shared effects of latitude and longitude, indicative of isolation by distance (Figure 3a–c, Figure 4). Although the four genetic clusters identified in Alcon suggest an important role for geography in delineating these groups, altitudinal and resistance differences among clusters are the dominant factors explaining genetic structure (Figure 3a, Table S4). Finally, geographical isolation played a limited but significant role in structuring the populations of Gentian and Myrmica, while landscape resistance seems to affect Alcon genetic structure both directly and through shared effects with altitude (Figure 4).

As expected from the complexity inherent to natural communities, a large part of the genetic structure remains unexplained (Figure 4) and could be partially due to biotic interactions which are most often ignored in landscape genetic studies. We thus examined the proportion of Alcon genetic structure co-varying with host genetic structure using co-inertia analysis. The resulting model (Table S4) demonstrates that substantial variation in Alcon genetic structure can be explained by host genetic structure (co-variation coefficient = 0.74**, Figure 3d, Table S3), corresponding to short arrows in the co-inertia graph (Figure 3d). Overall, most of the Alcon genetic variation co-varied with both hosts simultaneously (through co-inertia axis 1, representing 31.73% of all co-variation), indicating shared effects of Gentian and Myrmica genetic structure on Alcon genetic structure (Table S4). The second and third co-inertia axes were dominated by Alcon–Gentian and Alcon–Myrmica genetic costructure, respectively (Figure 3d, Table S4).

Whereas the degree of co-variation between Alcon and host genetic structure (arrow length) varied across space (Figure 3d), none of the co-variation (Table S4) could be explained by spatial variables and landscape resistance ($F_4 = 1.02$, $R^2_{adj} = 0.004\%$, $p = .371$), suggesting that other factors, most likely including co-evolution and shared dispersal, contribute to the genetic costructure. In addition, shared postglacial migration routes, which do not coincide with current levels of habitat fragmentation, may add to the observed levels of genetic parallelism.

4 | DISCUSSION

Theoretical predictions of community dynamics point to adverse effects of habitat fragmentation on species' interaction networks, yet empirical validation directly from the field was still lacking. Through integrating landscape ecology, population genetics and field monitoring of a parasitic butterfly community module, we provide unique

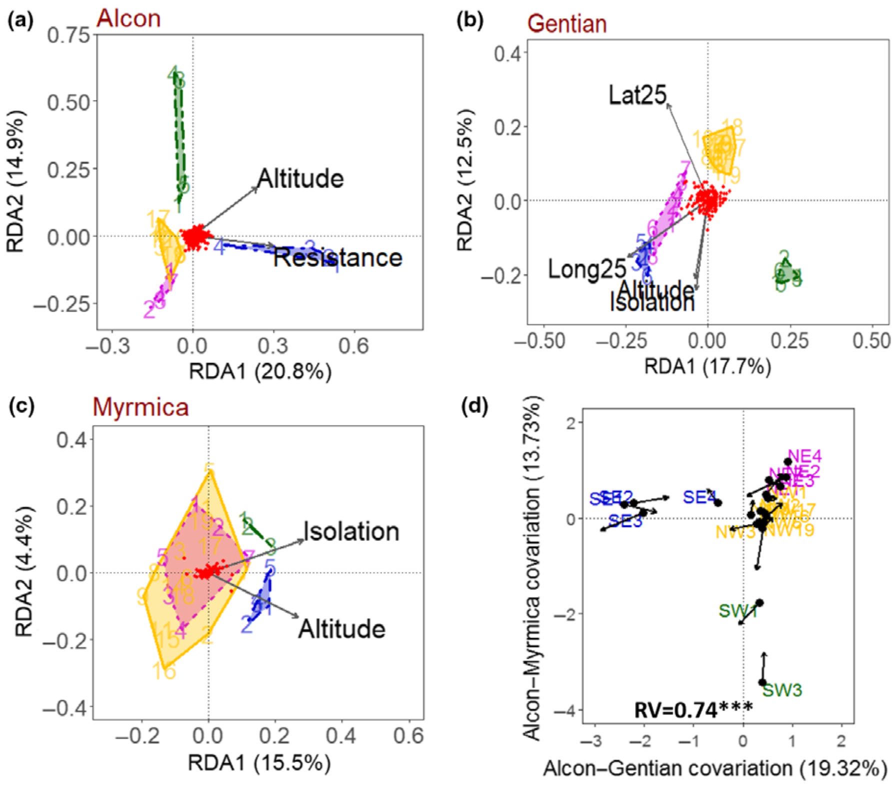

FIGURE 3 Role of environmental factors and host genetic structure contributing to the Alcon genetic structure. (a–c). Triplots representing the genetic structure of Alcon, Gentian and Myrmica, respectively, and the abiotic factors significantly contributing to this structure (Table S4). Colours correspond to spatial structure in Figure 1d. Red dots represent SNP loadings onto the two most dominant RDA axes. Total number of RDA axes is two, four and two, for Alcon, Gentian and Myrmica, respectively (see Table S4). (d) Genetic costructure between Alcon and hosts. The graph represents the second and third co-inertia axes representing co-variation with Gentian and Myrmica genetic structure, respectively. The first axis represents co-variation with both host species simultaneously (shared co-variation, Table S4). The first five axes of the co-inertia analyses explained a total of 74.93% of the co-variation between the Alcon genetic matrix and the host genetic matrix (Table S4). Length of arrows is proportional to divergence between Alcon genetic structure and host genetic structure (shorter arrows are equivalent to stronger costructure). For example, SW3 is featured by high co-variation between Alcon and Gentian (along *x*-axis), but strong divergence between Alcon and Myrmica (along *y*-axis) [Colour figure can be viewed at wileyonlinelibrary.com]

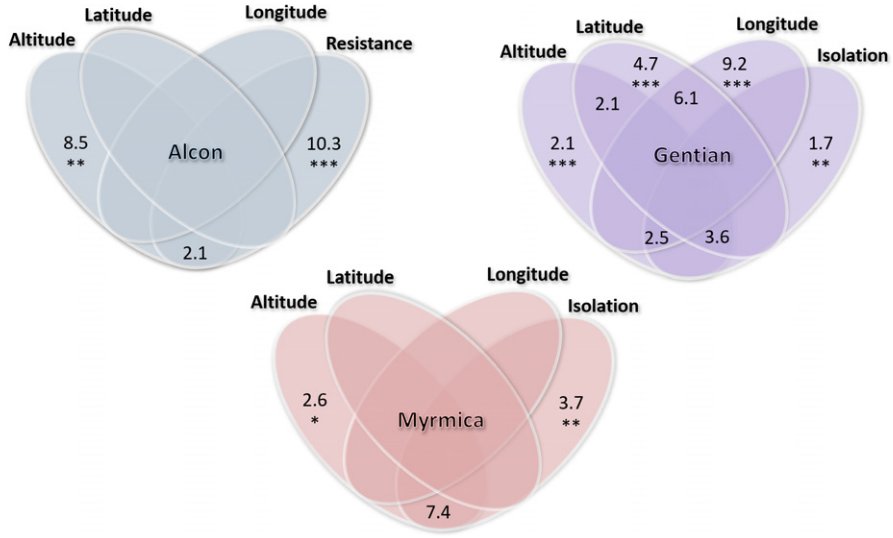

FIGURE 4 Venn diagram showing unique and common abiotic contributions (R^2_{adj}) to Alcon, Gentian and Myrmica genetic structure. Values were obtained through redundancy analyses with variation partitioning. Only common contributions >2% are shown. Significance of unique fractions obtained through partial RDA analysis: *$p < .05$, **$p < .01$, ***$p < .001$ [Colour figure can be viewed at wileyonlinelibrary.com]

insights in the impacts of habitat fragmentation on the genetic diversity and structure of strongly interacting species. We demonstrate that habitat fragmentation impacts within-population genetic diversity and among-population genetic structure of Alcon. Alcon and its two interacting species show striking parallelism in their genetic structure, but neither spatial variables nor fragmentation of the butterfly habitat explain this genetic costructure. We discuss the eco-evolutionary implications that are specific to the study system, as well as global conservation concerns arising from this study.

4.1 | Abiotic drivers of genetic diversity and structure in three interacting species

Because habitat fragmentation deteriorates landscape connectivity through reductions in the amount of habitat suitable for dispersal and breeding, and through increased geographical distance among breeding sites, it typically disrupts the genetic integrity of butterfly populations (Thomas, 2016). In line with this unfavourable trend, we found that increased landscape resistance increased the genetic distance between the Alcon populations under study (Figure 2). This finding is consistent with the relatively localized dispersal events observed during capture–mark–recapture monitoring (Figure S1). By hindering butterfly movements across the landscape to various extents, habitat fragmentation thus resulted in a spatial mosaic of highly and poorly connected sites (Figure 1d). This connectivity loss further led to a marked decrease in butterfly genetic diversity (Figure 2a), implying a harmful effect of habitat fragmentation on its population dynamics. In line with this finding, habitat fragmentation has frequently been shown to impact genetic processes and population dynamics in butterfly species (Fountain et al., 2016; Keyghobadi, Roland, & Strobeck, 2005; Krauss, Schmitt, Seitz, Steffan-Dewenter, & Tscharntke, 2004).

Alcon and Gentian genetic diversity declined with increasing altitude (Figure 2b). Because census population sizes did not follow an altitudinal pattern, this result can be attributed to historical post-glacial migration to higher altitudes followed by population expansion. Whereas relations between latitudinal historical range shifts and population genetic diversity have been frequently observed (e.g., Eckert, Samis, & Lougheed, 2008; Guo, 2012; Schär et al., 2017), far less evidence exists for historical migration effects on genetic patterns along elevation gradients. Dispersal limitation and obligatory dependence of Alcon on its host plant further explains the stronger altitude effect for Alcon than for the Gentian (Figure 2b), through slower and more recent uphill migration. The lack of a similar altitudinal signature across the Myrmica populations can be due to high dispersal and colony founding rates, which is in line with the lack of genetic structure observed in this species relative to the other species (Figure 3). Species-specific differences in migration histories should, however, be treated as potential hypotheses to be tested in further studies.

Strong parasitic pressure on host populations due to high Alcon population sizes or gene flow could give rise to demographic bottlenecks in host populations, resulting in low genetic diversity of parasitized host populations. On the other hand, if traits associated with co-evolution (e.g., phenology, chemical signature and coloration) are featured by complex genetic architectures, parasite-mediated selection may act on genomewide genetic diversity, resulting in high overall genetic diversity of parasitized populations (Bérénos, Wegner, & Schmid-Hempel, 2010). Given the absence of a negative (antagonistic) correlation between Alcon and host genetic diversity (Figure 2c), our results suggest limited parasitic impact of Alcon on its two host species. Moreover, the genetic diversity of the hosts was not significantly affected by Alcon density (Figure 2d), indicating that the hosts are not markedly impacted by Alcon population dynamics. Importantly, this also suggests that conservation efforts aiming to increase connectivity for butterflies would maintain the functioning of the community module without compromising the host species.

Latitude, longitude, altitude and landscape resistance all contributed to the genetic structure in the community, to an extent that varied considerably among species (Figures 3a–c, S6). The particularly strong effect of landscape resistance on Alcon genetic structure (10.3%, Figure S6) may imply both direct and indirect (host-related) effects of spatial configuration on Alcon genetic structure. Indeed, a specific set of host genotypes will attract co-evolved, rather than maladapted, parasite individuals (Räsänen & Hendry, 2008; Thompson & Burdon, 1992). Changes in host genetic structure driven by spatial factors may therefore impose changes in Alcon genetic structure on top of the direct effects of spatial configuration on Alcon genetic structure. This finding suggests that changes in spatial configuration (e.g., through land use changes) may impact various genetic processes underlying community dynamics.

4.2 | Genetic parallelism between parasite and hosts

A high degree of genetic parallelism within the community module resulted in strong co-inertia between butterfly and host genetic structure. Interestingly, and in agreement with the distinct spatial effects observed in Figure 3a–c, this costructure could not be explained by spatial variables. We suspect that reciprocal co-evolutionary selection between Alcon and its two hosts has synchronized the genetic structure of the host–parasite module through reducing effective gene flow between communities. Specifically, the absence of landscape resistance (thus potential gene flow) effects on genetic costructure may imply that co-evolution itself drives effective gene flow. It is well known that local adaptation (including local co-evolution) inhibits effective gene flow through low fitness and low reproductive ability of immigrating (nonlocal) individuals (Kawecki & Ebert 2004). The notion of co-evolution in our study system is concordant with previously documented co-evolutionary shifts in flower phenology (*Gentiana pneumonanthe* plants) and surface chemistry (*Myrmica* ants) to escape local infestation by *Phengaris alcon* butterflies (Nash et al., 2008; Valdés & Ehrlén, 2017). Where postponed plant flowering and altered ant surface chemistry prevent reproduction of desynchronized butterfly immigrants, local co-evolution has the potential to increase the genetic distance between communities, resulting in parallel genetic structure among the interacting species. We conclude that spatial community structure may provide opportunities for co-evolution, while frequent local butterfly immigration (under high landscape connectivity) maintains relatively high levels of genetic diversity within meta-populations. Partial overlap in current dispersal pathways and parallel postglacial migration routes may also result in similar genetic structure. However, experimental manipulation of the community modules is required to disentangle the contributions of co-evolution *versus* shared dispersal pathways to genetic costructure and community functioning.

4.3 | Ecological implications of in situ meta-community dynamics

Our study does not capture causal relationships between landscape connectivity and community dynamics, but it does provide preliminary perspectives on the strength of in situ species' associations under threat of habitat fragmentation. The presumably important role of co-evolutionary processes in shaping genetic parallelism among the three interacting species, in concert with strong effects of habitat fragmentation on genetic diversity and structure in the focal and most threatened species, could point to unknown impacts of landscape configuration on co-evolutionary dynamics. Although spatial variables did not affect genetic costructure, further research should therefore aim to study the indirect impacts of habitat fragmentation on costructure and community dynamics, as landscape configuration could mediate the impact of host genetic variation on Alcon genetic structure.

Reconnecting isolated communities could restore community dynamics (including co-evolutionary processes) and simultaneously improve local Alcon genetic diversity and population persistence. Interestingly, relatively dense Alcon populations with high genetic diversity did not leave a noticeable mark on host genetic diversity despite the well-known adverse effects that *P. alcon* can have on *Myrmica* nests (Nash et al., 2008). The gradual and reciprocal accumulation of co-evolutionary genetic signatures over time may have allowed coexistence without strong fluctuations in parasite and host genetic diversity. Building on this finding, we emphasize the strength of community genetic studies in detecting eco-evolutionary signatures that have been shaped over contemporary time periods. However, because regional sampling does not necessarily reflect rangewide genetic structure and parallelism patterns, we acknowledge that the transferability of our conclusions to other regions and taxa is limited. To shed light on the global extent of our findings, it would be insightful to deploy the used integrative strategy, combining pooled sequencing and multivariate genetic approaches, in other natural settings and where possible combined with experimental tests. Although a pooled sequencing approach complicates the generation of genetic marker-specific inferences (Figure S3), it offers major advantages for studying in situ community dynamics. The study of population genetic variation of multiple species in a meta-community framework easily requires thousands of DNA samples. Pooled sequencing could allow genotyping hundreds of populations with modest research budgets, and multivariate techniques subsequently allow disentangling the relative contributions of abiotic and biotic drivers of community dynamics.

Predicting how species will cope with global environmental changes is a key ambition in evolutionary and ecological sciences. However, the lack of eco-evolutionary integration in forecasting models may compromise their ability to predict range dynamics and to provide realistic guidelines for sustainable conservation (Ikeda et al., 2017; Lavergne, Mouquet, Thuiller, & Ronce, 2010). We stress that ignoring the impacts of widespread co-evolutionary networks on the ability of species to cope with global environmental changes may affect outcomes of conservation strategies and forecasting models to an unknown extent. Moreover, the combined impacts of multiple global environmental changes on community dynamics are expected to be distressing, but have yet to be assessed.

5 | CONCLUSIONS

Natural communities under threat of habitat fragmentation are predicted to suffer from reduced dispersal opportunities, which in turn may disturb genetic patterns within and among interacting species. Our findings are largely in line with this prediction and encourage research involving meta-community-wide genetic analysis and in situ observations, where feasible in combination with an experimental approach. Conservation actions aiming at increasing connectivity in the landscape could prevent dispersal to fall beyond critical levels and stabilize meta-community dynamics. We argue that co-evolutionary interactions, including plant–pollinator, host–parasite and mutualistic interactions, render species more prone to the consequences of global environmental changes through direct and indirect impacts on the population dynamics of species depending on the presence of vital host populations.

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DATA ACCESSIBILITY

SNP allele frequencies with flanking sequences and the pairwise resistance matrix are archived at Dryad (https://doi.org/10.5061/dryad.f371754).

AUTHOR CONTRIBUTIONS

H.D.K. wrote the manuscript, assisted with sampling and performed the laboratory work and data analyses. V.S. and M.B. provided the context of the project and supervised. J.G.P. performed the bioinformatics, and M.T. located the community sites and introduced the study system. C.T. assisted with the analysis of the field surveys, and J.M. assisted with sampling. All co-authors also commented on the manuscript.

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