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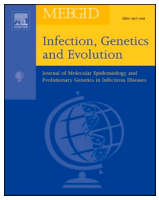

Genetic diversification of an invasive honey bee ectoparasite across sympatric and allopatric host populations

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ABSTRACT

Invasive parasites are major threats to biodiversity. The honey bee ectoparasite, *Varroa destructor*, has shifted host and spread almost globally several decades ago. This pest is generally considered to be the main global threat to Western honey bees, *Apis mellifera*, although the damages it causes are not equivalent in all its new host's populations. Due to the high virulence of this parasite and the viruses it vectors, beekeepers generally rely on acaricide treatments to keep their colonies alive. However, some populations of *A. mellifera* can survive without anthropogenic mite control, through the expression of diverse resistance and tolerance traits. Such surviving colonies are currently found throughout the globe, with the biggest populations being found in Sub-Saharan Africa and Latin America. Recently, genetic differences between mite populations infesting surviving and treated *A. mellifera* colonies in Europe were found, suggesting that adaptations of honey bees drive mite evolution. Yet, the prevalence of such co-evolutionary adaptations in other invasive populations of *V. destructor* remain unknown. Using the previous data from Europe and novel genetic data from *V. destructor* populations in South America and Africa, we here investigated whether mites display signs of adaptations to different host populations of diverse origins and undergoing differing management. Our results show that, contrary to the differences previously documented in Europe, mites infesting treated and untreated honey bee populations in Africa and South America are genetically similar. However, strong levels of genetic differentiation were found when comparing mites across continents, suggesting ongoing allopatric speciation despite a recent spread from genetically homogenous lineages. This study provides novel insights into the co-evolution of *V. destructor* and *A. mellifera*, and confirms that these species are ideal to investigate coevolution in newly established host-parasite systems.

1. Introduction

Invasive species represent major threats to our ecosystems and economy (Dunn and Hatcher, 2015; Essl et al., 2011; Marbuah et al., 2014; Pyšek and Richardson, 2010). Understanding their dispersal abilities and the mechanisms shaping their adaptation potential in their new ranges can help to prevent additional invasions and mitigating the damages they cause (Banks et al., 2015; David et al., 2017; Hulme, 2009). The mite *Varroa destructor* (Anderson and Trueman, 2000) is an ectoparasite that originally infested colonies of the Eastern honey bee

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(*Apis cerana,* Fabricius, 1793) in Asia (Anderson and Trueman, 2000; Chantawannakul et al., 2016; de Jong et al., 1982). However, after successfully spilling over to introduced colonies of the Western honey bee (*Apis mellifera,* Linnaeus, 1758) in North-East Asia, this parasite managed to spread outside its original distribution range and to invade almost the entire range of its new host, which is distributed almost globally (Martin et al., 2012; Traynor et al., 2020). Acting as a vector of honey bee viruses (McMenamin and Genersch, 2015; Wilfert et al., 2016), *V. destructor* is nowadays considered to be the main biotic threat to *A. mellifera* (Le Conte et al., 2010; Moritz et al., 2005; Neumann and Carreck, 2010).

Despite the recent invasion and ubiquity of the parasite, not all populations of *A. mellifera* have been impacted similarly by *V. destructor*. For example, infestations with the mite in native European and European-derived Western honey bee lineages usually lead to devastating levels of mite population growth, causing the host colonies to succumb within one or two years (Calis et al., 1999; Martin, 1998). Interestingly, a few populations of European or European-derived *A. mellifera* have adapted to the mite, through natural selection or selective breeding (Büchler et al., 2010; Le Conte et al., 2007; Locke, 2016; Rinderer et al., 2010; Seeley, 2006). These "surviving populations" manage to keep parasite levels and damages under critical thresholds by the expression of a diversity of parasite resistance or tolerance traits (Kurze et al., 2016; Mondet et al., 2020). Such resilience to *V. destructor* infestations is also observed in *A. mellifera* subspecies native to sub-Saharan Africa (Nganso et al., 2017; Pirk et al., 2016; Strauss et al., 2014), as well as some African-derived populations (Camazine, 1986; Guzman-Novoa and Sanchez, 1996; Medina-Flores et al., 2014). But despite these cases of surviving populations, resistance or tolerance traits are absent or not sufficiently expressed in the great majority of Western honey bee populations around the globe. Beekeepers managing such susceptible colonies must generally use intensive acaricide treatments to keep the parasite populations below lethal thresholds (Rosenkranz et al., 2010).

South America is a unique place to study the interactions between *V. destructor* and *A. mellifera* as several lineages of the host with different levels of resilience to mite infestations co-exist in that continent. Although the Western honey bee is not native to South America, a diversity of *A. mellifera* lineages have been introduced there (Nelson et al., 2017; Wallberg et al., 2014). The first honey bees that were imported there were of European origins (*A. m. mellifera* and *A. m. ligustica*) (Bierzychudek, 1979). Additionally, African honey bees (*A. m. scutellata*) were introduced in Brazil in 1956. This introduction resulted in the quick spread of this lineage, and introgression between the different subspecies (Michener, 1975). Today, the resulting "Africanized" hybrids have spread to most countries of the continent, but climatic and environmental factors limit their dispersal towards the southern regions of South America. Notably, Africanized hybrid colonies are found throughout most of Uruguay and the northernmost parts of Argentina (Branchiccela et al., 2014; Porrini et al., 2019), and display high resilience levels against *V. destructor* infestations (Mendoza et al., 2020; Rosenkranz, 1999).

In contrast to the diversity of hosts, *V. destructor* populations found in South America and other parts of its invasive range are genetically homogenous. In fact, pioneer work on *V. destructor* genetics suggested that only two lineages of mites from North-East Asia displaying a "quasi-clonal" genetic structure managed to leave their natural distribution (Anderson, 2000; Anderson and Trueman, 2000; Solignac et al., 2005). This low diversity was linked with bottleneck events associated with the host jump and further dispersal of the mite, and with the peculiar incestuous mating of the mite. Yet, several subsequent studies have described lineage admixture as well as significant levels of genetic differentiation within and between mite populations infesting *A. mellifera* (Beaurepaire et al., 2017b, 2017a; Dietemann et al., 2019; Dynes et al., 2017; Zheng et al., 2022). Given that *V. destructor* has a relatively short generation time (*i.e.*, about a month) (Rosenkranz et al., 2010) compared to a honey bee colony (*i.e.*, typically living several years), and that the parasite has started to invade the world several decades ago, the observed significant levels of genetic differentiation may be signs that mite populations have started adapting to their local new host populations. Notably, such adaptations would be expected under co-evolutionary arms races between hosts and parasites. Under these assumptions, selective forces are expected to lead to the swift emergence of adaptations (Paterson et al., 2010). These forces are expected to be stronger in parasites, because of their shorter generation time compared to their hosts (Ebert, 1994; Gandon and Michalakis, 2002), and may take different directions in spatially distant parasite populations, potentially leading to mosaics of co-evolution (Thompson, 2005; Thompson and Cunningham, 2002).

Understanding the selective pressures affecting the emergence of adaptations to different honey bee populations in *V. destructor* is crucial to enhance the fundamental knowledge on this important pest and better understand how to mitigate its impact. Environmental conditions within *A. mellifera* colonies are very similar across the host's distribution range due to homeostasis (Stabentheiner et al., 2021), and therefore not likely to represent a strong selective pressure on their parasites. In contrast, the expression of host resistance traits in colonies infested by the mites kept under natural selection pressure might play an important role because these host traits can significantly impact the parasite's fitness (Eliash and Mikheyev, 2020; Neumann and Blacquière, 2016). In parallel, mites from regularly treated honey bee colonies may develop adaptations to the acaricides used (González-Cabrera et al., 2018; Milani, 1999). In that case, it can be expected that significant levels of genetic differentiation will be detectable in mites infesting different host populations under diverse pest management regimes (*e.g.*, with and without treatments) (de Meeûs et al., 2007; Gandon et al., 2008; Mazé-Guilmo et al., 2016). Finally, parasite dispersal, *e.g.*, through transportation of honey bee colonies by beekeepers, may disrupt local adaptation scenarios and could result in homogeneous parasite populations across spatially separated host populations despite high host-related selective pressures (Boulinier et al., 2016; Criscione et al., 2005).

Several studies recently provided genotypic or phenotypic evidence for the emergence of adaptations in *V. destructor* infesting different treated and untreated *A. mellifera* populations in Europe (Beaurepaire et al., 2019; Moro et al., 2021a, 2021b). We here tested whether genetic changes can be detected in other populations of *V. destructor* infesting *A. mellifera* in order to further investigate the factors affecting the adaptation of this parasite in its invasive range. More precisely, we tested whether adaptations to different host populations can cause mite genetic diversification by analyzing the population genetics of *V. destructor* mites infesting introduced European and Africanized honey bee colonies in South America, and comparing them to mites infesting native populations of honey bees in Africa (South Africa) and Europe (France). Altogether, this study provides novel insights into the coevolution between *V. destructor* and its new host, and into natural and anthropogenic factors influencing parasite adaptations.

2. Material and methods

2.1. Sampling

Adult *V. destructor* females were collected using the powdered sugar and bottom board methods (Dietemann et al., 2013) in Argentina, Uruguay, France and South Africa (Fig. 1), in different groups of *A. mellifera* colonies consisting of bees of distinct origins and/or different mite management practices (Table 1).Some of the colonies used in this study originated from naturally mite-surviving population, *i.e.*, groups colonies that can survive without the need for treatment against mites by means of natural selection (Le Conte et al., 2007; Mendoza et al., 2020; Strauss et al., 2014). Here, these colonies were labelled as "untreated" (Table 1). The data from France were previously published in Moro et al. (2021a), but two additional markers were included in the current

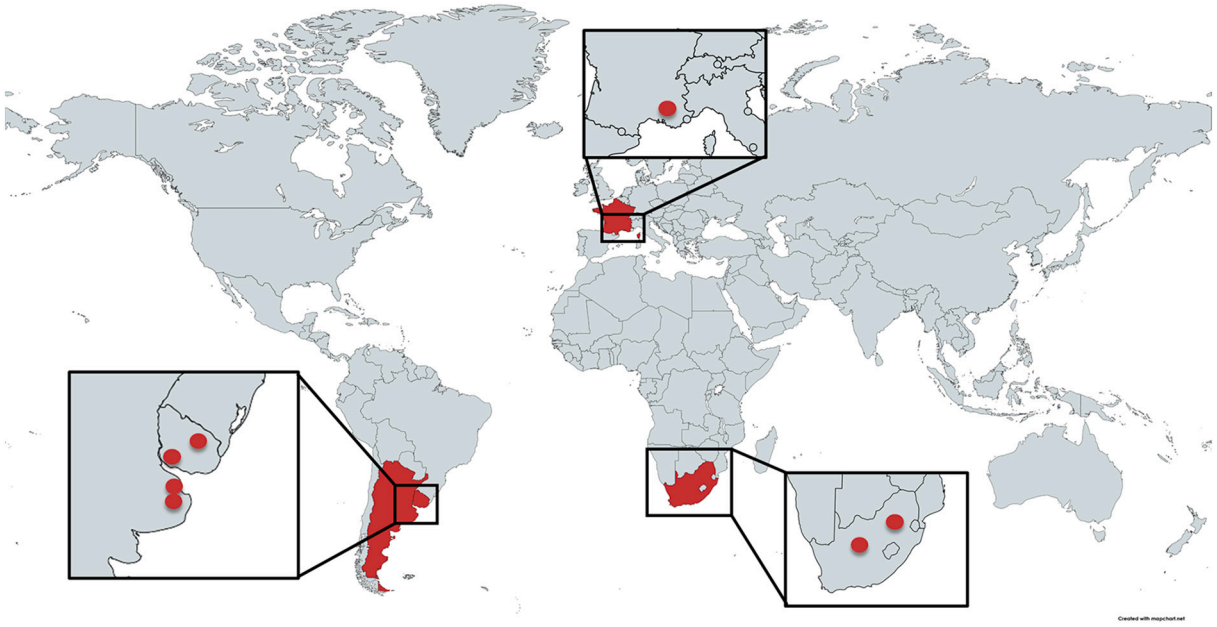

Fig. 1. Location of sampling sites.
Map representing the approximate location of the study sites (red circles), see Table 1 for GPS coordinates. Image made with mapchart.net.

Table 1
Information on the samples and genetic estimates.

Country	Region	GPS	Host	$N_{colonies}$	N_{mites}	NA	R	HO
Uruguay	Treinta y Tres	33°15′16.2"S 54°25′34.1"W	Africanized (UT)	6	139	2.33 (0.33)	1.96 (0.09)	0.04 (0.02)
	Colonia	34°20′17.5"S 57°41′25.9"W	European (T)	6	135	2.44 (0.41)	1.77 (0.13)	0.03 (0.01)
Argentina	Vieytes	35°14′17.42"S 57°38′26.589"W	European (UT)	6	81	2.00 (0.17)	1.67 (0.20)	0.04 (0.01)
	La Plata	34°54′40.2"S 57°55′37.2"W	European (T)	7	130	2.89 (0.26)	1.56 (0.19)	0.06 (0.02)
France*	Avignon	43°54′56.3"N 4°52′39.4″E	European (UT)	6	129	2.22 (0.32)	1.69 (0.14)	0.02 (0.01)
	Avignon	43°54′56.3"N 4°52′39.4″E	European (T)	6	121	1.89 (0.20)	1.75 (0.17)	0.02 (0.01)
South Africa	Pretoria	25°45′16.9"S 28°13′51.0″E	*A. m. scutellata* (UT)	10	75	1.89 (0.35)	1.28 (0.12)	0.01 (0.01)
	Kalahari	29°01′41.5"S 23°46′57.1″E	*A. m. scutellata* (UT)	5	17	1.11 (0.11)	1.11 (0.11)	0.01 (0.01)

Information about the origin of the *V. destructor* analyzed and sample size: country of sampling, region of sampling, GPS coordinates, dominant lineage of *A. mellifera* (Host) according to morphological and behavioral together with treatment regime between parentheses (UT: untreated, T: treated in Fall with Amitraz, Apivar®) and sample sizes (number of colonies and of mites per group). Additionally, the number of alleles (NA), allelic richness (R) and the level of observed heterozygosity (HO) are presented as mean across the loci (+/− SE)) in each group is given. *: samples from Moro et al. (2021a).

analysis (Suppl. Table 1).

2.2. Genotyping

The DNA of a total of 577 *V. destructor* samples (Table 1) was extracted using Chelex standard methods (Walsh et al., 1991) for the current study. 250 samples from France used in a previous study (Moro et al., 2021a) were also included (Table 1). A total of 8 microsatellite markers (Table S1) were used to genotype the samples following methods described in Beaurepaire et al. (2017b).

2.3. Analyses

The software GenAlex v 6.5 (Peakall and Smouse, 2012) was used to calculate several estimates of genetic diversity and population structure of mites. First, the number of alleles, the number of private alleles and the observed heterozygosity index were calculated across markers for each group and compared using Kruskal-Wallis tests using the software R v 3.6.1 (R Core Team, 2018). To display the genetic distance between mites infesting the different groups of honey bees, a PCA based on the mite genotypes was performed using the software R v 3.6.1. and the package Adegenet (Jombart, 2008; R Core Team, 2018). Additionally, the Jost D index (Dest) (Jost, 2008), an estimator reflecting genetic distance between groups (Whitlock, 2011), was calculated using the same software to compare mites infesting the different groups of honeybee colonies. Finally, to analyze the population structure of *V. destructor* across samples from the different continents (South America: Uruguay and Argentina, Europe: France and Africa: South Africa) and between groups of colonies (*e.g.*, treated or not) within each region, an Analysis of Molecular Variance (AMOVA) was conducted using GenAlex v 6.5.

3. Results

The number of alleles differed significantly across the groups of *V. destructor* sampled (Kruskal-Wallis test, H = 21.142, p = 0.003) (Table 1). When running a post-hoc Dunn test to conduct a pairwise comparison between the mite groups, the group from the Kalahari Desert differed significantly from the rest (all *p-values* < 0.05). However, a lower sample size was analyzed in this group (N = 17) and may have caused the observed difference. Removing this group, the number of alleles was no longer significantly different across all groups (Kruskal-Wallis test, H = 8.683, p = 0.192), showing that the reduced sample size indeed affected the first tests. In parallel, the heterozygosity levels did not differ significantly across the eight groups (Kruskal-Wallis test, H = 11.326, p = 0.125) (Table 1).

The PCA analysis revealed a clear segregation between some groups of mites (Fig. 2) based on the first two principal components. The first component, representing 26.23% of the total variance, clustered well the samples from France and the other six groups, while the second component, representing 15.27% of the variance, separated the samples from South Africa from the rest.

In parallel, the analyses of genetic distance across mite groups revealed specific patterns of genetic differentiation between the *V. destructor* groups compared (Table 2). Notably, the highest genetic distance values obtained were between the groups from South Africa and France (average D_{est} = 0.309), whereas the values obtained when comparing groups from the same countries were low (average D_{est} = 0.007), albeit sometimes significant. The South American mite groups (Uruguay and Argentina) were not highly differentiated (average D_{est} = 0.010), but the differences between these parasites and the samples from France (average D_{est} = 0.138) and South Africa (average D_{est} = 0.154) were an order of magnitude higher.

Finally, the AMOVA revealed that the genetic differences of mites across the three continents were responsible for a substantial amount of the genetic variation (33%, p-value <0.05), while the differences between groups of colonies within these continents were much smaller (3%, p-value <0.05) (Table 3). Yet, the majority of genetic variation was associated with the differentiation between individuals in each group (64%, p-value <0.05).

4. Discussion

In this study, analyses of the population genetics of invasive *V. destructor* mites infesting colonies of their novel host, *A. mellifera,* revealed distinct levels of genetic differentiation of the parasite across honey bee populations. Most notably, the findings documented here show that, although the parasite populations have originated from highly homogenous source populations that started invading the world a few decades ago (Solignac et al., 2005), they have now diversified significantly.

Due to its incestuous mating system and recent worldwide spread from a restricted number of source populations, *V. destructor* populations were initially suggested to be composed of pseudo-clonal individuals in the invasive range of the parasite (Solignac et al., 2005). Yet, several recent studies conducted outside of Asia (*i.e.*, in the invasive range of the mite) have shown that *V. destructor* populations display significant levels of genetic diversification at varying geographical scales (Beaurepaire et al., 2019; Dynes et al., 2017; Moro et al., 2021a). Here, our results confirm these findings, also revealing significant genetic differentiation across population of mites within and between the locations compared, in spite of an overall low numbers of alleles and heterozygosity.

The experimental design used in this study, including paired honey bee groups in each of the investigated region, allowed comparing *V. destructor* populations over different levels: between distant regions of the world, as well as within these regions across host groups (*i.e.*, colonies differing in their mite management regimes and/or host lineages). First, the differences between mites infesting honeybee colonies across the different regions was responsible for about a third of the total genetic variation of the dataset. This suggests that, despite common origins, *V. destructor* populations in these three continents are evolving in allopatry, and that no or limited further exchanges of mites between these areas have occurred in the recent past.

The second level of variation compared allowed investigating the differentiation of mites between host groups located in the same environment. The absence of difference between mites in the two South African honey bee groups differ from the previous results from France (Moro et al., 2021b). Our sampling design only allowed comparing a restricted number of colonies in a few apiaries per region, which was nevertheless sufficient to show genetic differentiation in European populations (Moro et al., 2021a). While we cannot exclude that genetic differences could have been detected when adding more sampling sites and/or more distance between the populations studied here, some specific host or management factors might have prevented parasites from differentiating. For instance, African *A. mellifera* colonies are known to swarm and migrate readily (Hepburn and Radloff, 1998; Pirk et al., 2016), thereby facilitating parasites transmission over long distances and resulting in the maintenance of high gene flow levels across mites infesting colonies in geographically distant areas. In the case of the South American populations (Uruguay and Argentina), the absence of a strong genetic structuring of the mites of this region suggests that all mites sampled in this study is congruent with the predominance of a

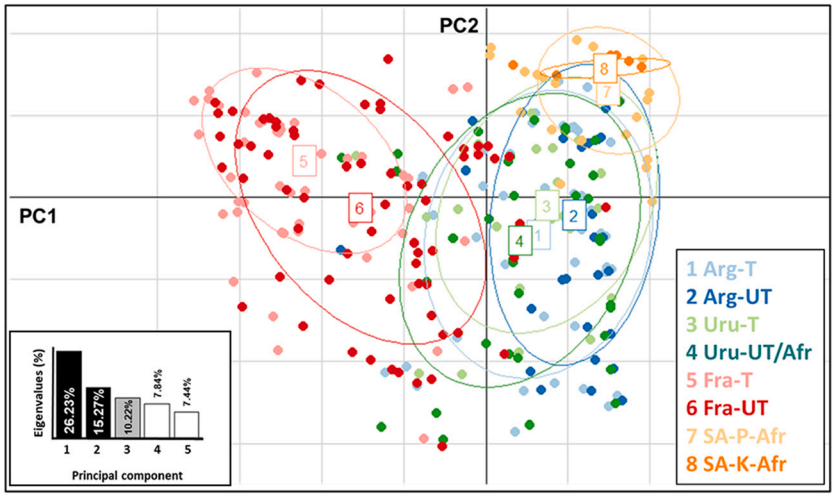

Fig. 2. Analysis of population structure of *V. destructor*. Principal Component Analysis based on the genotype of mites infesting different *A. mellifera* groups (color-code: see legend; countries: Arg: Argentina, Uru: Uruguay, Fra: France, SA: South Africa; P: Pretoria; K: Kalahari; groups: T: Treated, UT: Untreated, and Afr: African(ized)). The first two Principal components are displayed (PC1 = 26.23%, PC2 = 15.27%).

Table 2
Pairwise genetic differentiation across *V. destructor* groups.

	Arg_T	Arg_UT	Uru_T	Uru_UT	Fra_T	Fra_UT	SA_PR	SA_K
Arg_T		n.s.	n.s.	*	*	*	*	*
Arg_UT	0.007		*	*	*	*	*	*
Uru_T	0.006	0.010		*	*	*	*	*
Uru_ UT	0.008	0.023	0.006		*	*	*	*
Fra_T	0.164	0.202	0.153	0.138		*	*	*
Fra_ UT	0.106	0.149	0.106	0.083	0.016		*	*
SA_PR	0.165	0.149	0.140	0.164	0.319	0.298		n.s.
SA_K	0.164	0.149	0.140	0.164	0.321	0.300	0.000	

Bottom-left: Dest index, reflecting the genetic distance across the groups. Upper-right: significance of the tests (*: significant, n.s.: non-significant) after multiple testing corrections (Bonferroni). Names are composed of the colony of origin (Arg: Argentina, Uru: Uruguay, Fra: France, SA: South Africa) and group (T: Treated, S: Surviving) or location for South Africa (PR: Pretoria, K, Kalahari).

Table 3
Results of the Analysis of Molecular Variance (AMOVA).

Level	d.f.	Est. Var.	%	*p*-value
Among regions	2	0.536	33%	<0.05
Among populations	5	0.055	3%	<0.05
Within populations	1646	1.050	64%	<0.05
Total	1653	1.641	100%	

Different levels of comparison, including differences between regions (South American, South African and French populations), among populations (between groups of honeybee colonies in each region) and within populations. The degrees of freedom (d.f.), estimated variance (Est. Var.), percentage of variation (%) and *p*-values are provided for each group and overall.

single invasive lineage of the mite, as suggested previously (Maggi et al., 2012; Strapazzon et al., 2009). Moreover, the results obtained when calculating D_{est} estimates across paired host groups of samples in Uruguay and Argentina did not reveal particular structuring of *V. destructor* populations between the Africanized and European-derived host lineages. These data suggest an ongoing gene flow between parasites infesting colonies of Africanized and European-derived honey bees. Moreover, the lack of genetic differentiation between treated and untreated *A. mellifera* colonies in Uruguay and Argentina also suggests an ongoing strong gene flow between parasite populations infesting these host groups. Notably this finding contrasts with results found previously in Europe (Beaurepaire et al., 2019; Moro et al., 2021a). Given that the different host populations studied here were all first exposed to the parasite a few decades ago, this discrepancy might not be caused by different co-evolutionary periods. Instead, this observation might have rather been caused by the expression of different host resistance or tolerance traits in the populations, or different management factors which were not controlled for in the current study. Notably, further investigations of the potential role of host resistance traits and their possible impact on mite population genetics in South America and Europe are underway.

Finally, the finer level of analysis of the genetic structure of *V. destructor* populations revealed a substantial diversity of mite genotypes within every host groups, as shown by the AMOVA and also visible on the PCA. This result confirms previous ones documenting a dynamic population structure of *V. destructor* mites, probably led by the rapid fixation of rare mutations due to inbreeding followed by subsequent admixture *via* genetic recombination taking place when foundress mites co-infest host cells (Beaurepaire et al., 2017b).

To conclude, our results show that *V. destructor* populations infesting *A. mellifera* across the Atlantic Ocean differ substantially, although these invasive populations are known to originate from the same source. These results illustrate well how coevolution can drive the rapid genetic differentiation of invasive species (Ebert, 1998; Paterson et al., 2010). These findings also call for follow-up studies aiming at comparing distinct mite population to decipher the mechanisms driving these differences, and about the impact of mite divergence on honey bee health, *e.g.*, whether different mite genotypes interact differently with varroa-transmitted viruses.

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CRediT authorship contribution statement

Alexis Beaurepaire: Conceptualization, Methodology, Data curation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing, Funding acquisition. **Daniela Arredondo:** Formal analysis, Data curation, Investigation, Visualization, Writing – review & editing. **María Laura Genchi-García:** Formal analysis, Data curation, Investigation, Writing – review & editing. **Loreley Castelli:** Investigation, Writing – review & editing. **Francisco Jose Reynaldi:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Karina Antunez:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Ciro Invernizzi:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Fanny Mondet:** Conceptualization, Writing – review & editing, Funding acquisition. **Yves Le Conte:** Conceptualization, Writing – review & editing, Supervision, Funding acquisition. **Anne Dalmon:** Conceptualization, Writing – review & editing, Project administration, Supervision, Funding acquisition.

Declaration of Competing Interest

None.

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