Original Article

Head morphology reflects the introduction history in a globally invasive carnivore—the small Indian mongoose

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ABSTRACT

Species displaced outside their native range may face new pressures resulting from both environmental gradients and important differences in ecosystem structure. We investigated how this may impact the morphological variation of a globally introduced carnivoran, the small Indian mongoose. Previous research showed size variations in several introduced populations, suggesting that these differences resulted from character release in response to the absence of competition from native species. Here, we contrasted the morphological evolution of indigenous and introduced populations using geometric morphometric approaches on the head system of a large sample of specimens belonging to several regions. Our analyses revealed that differences in size and shape between introduced and native populations do not support hypothesis of character release. These results suggest that morphological variations in introduced populations may reflect the introduction history of the species, rather than evolutionary processes resulting from changes in ecosystem composition.

Keywords: invasive species; *Urva auropunctata*; geometric morphometrics; head morphology; character release; introduction history

INTRODUCTION

Over the past centuries, increased worldwide human activities and trade have dramatically promoted changes in ecological structure (Dayan and Simberloff 1998), through direct modifications of the environment, but also by favouring introductions of plant and animal species outside their natural boundaries (Perrings *et al.* 1992, Hulme 2009). As such, exotic species, defined as species introduced outside their native range, may settle and spread, negatively impacting autochthonous ecosystems, and consequently be considered invasive. As a result, biological invasions are now recognized as one of the major drivers of loss of global biodiversity (Bellard *et al.* 2016a, b, Holmes *et al.* 2019). Among all environments, islands are particularly threatened by the introduction of exotic species. Indeed, these peculiar ecosystems are often composed of endemic and specialized species that have evolved in isolation, with few or no predators (Banks and Dickman 2007, Medina *et al.* 2011, Doherty *et al.* 2016, Bellard *et al.* 2017, Spatz *et al.* 2017). Thus, the introduction of exotic species alters native populations and communities (Courchamp *et al.* 2003, Strauss *et al.* 2006, Watari *et al.* 2013), but can also have consequences for the intruders themselves, and may induce dramatic phenotypic and behavioural changes. Therefore, biological invasions represent interesting case studies of intraspecific phenotypic variation, especially in the context of the evolvability and adaptability of a population to new environments.

Ecology and morphology of exotic species introduced into islands can be particularly affected by changes in ecosystem composition, and notably by the decrease in competition pressure. Such phenotypic changes have been conceptualized as character displacement and character release (Dayan and Simberloff 1998, Losos 2000). Character displacement is defined as the accentuation of differences in traits under selection pressure of competition in closely related species whose distributions overlap, in order to avoid hybridization (reproductive character displacement) or resource use overlap (ecological character

displacement) (Brown and Wilson 1956). This concept also suggests that when a species occurs alone, it will acquire convergent traits with those of the other species. This phenomenon was termed as character release (Grant 1972). Character displacement and character release have been observed in several mammal species (Dayan and Simberloff 1998, 2005), including one of the most widely introduced carnivorans, the small Indian mongoose (Barun et al. 2015).

The small Indian mongoose, *Urva auropunctata* Hodgson, 1836, is a small carnivoran (between 300 and 650 g for adults) whose native distribution extends from Iraq to Myanmar, through Iran, Afghanistan, Pakistan, northern India, Nepal, and Bangladesh (Gilchrist et al. 2022) (Fig. 1). The species has been introduced into a large number of regions around the world between the late 19th and early 20th centuries: the Caribbean from 1870 to 1872, Hawaii in 1882, Fiji in 1883, the South American continent, and several islands in the Indian Ocean from 1900 onwards, and several Japanese and Croatian islands from 1910 onwards. These introduction events were mainly intentional, with the aim to limit the proliferation of rats in sugar-cane plantations and, in some instances, to eradicate the populations of native venomous snakes. Today, the small Indian mongoose is present on more than 60 islands around the world (Barun et al. 2013, Louppe et al. 2021b), and populations are expanding on the European continent in Croatia, Bosnia-Herzegovina, and Montenegro (Ćirović et al. 2011, Ćirović and Toholj 2016, Louppe et al. 2020).

In large parts of its native range, the small Indian mongoose is sympatric with three congeneric species, the Indian grey mongoose, *Urva edwardsii* Saint-Hilaire, 1818, the ruddy mongoose, *Urva smithii* Gray, 1837, and the crab-eating mongoose, *Urva urva* Hodgson, 1836, as well as several other small carnivorans. Conversely, the small Indian mongoose faces few or no competition pressures in most of its insular introduced range. Native carnivorans are absent from the Hawaiian, Fijian, and Japanese islands where the small Indian mongoose has been introduced. Nevertheless, in Trinidad, four native carnivorans are present: the Neotropical river otter, *Lontra longicaudis* Olfers, 1818, the crab-eating raccoon, *Procyon cancrivorus* Cuvier, 1798, the ocelot, *Leopardus pardalis* Linnaeus, 1758, and the tayra, *Eira barbara* Linnaeus, 1758. However, competition with the small Indian mongoose might be limited, as all these native species are much larger. In addition, the crab-eating raccoon and the ocelot are mainly nocturnal, and the Neotropical river otter does not share its habitat with the small Indian mongoose. Moreover, recent studies in two Caribbean islands showed that the presence of introduced domestic cats, dogs, and northern raccoons do not influence the distribution and the temporal activity of the small Indian mongoose (Louppe et al. 2021a).

Conversely, a native small carnivoran, the beech marten, *Martes foina* Erxleben, 1777, co-occurs in several Croatian islands where the small Indian mongoose has been introduced. Barun et al. (2015) showed that small Indian mongooses had shorter cranial lengths and smaller canine diameters in the three Adriatic islands where the species co-occurred, in comparison with specimens from other introduced populations worldwide where carnivorans of similar ecology are absent. The authors suggested that these differences might reflect character release
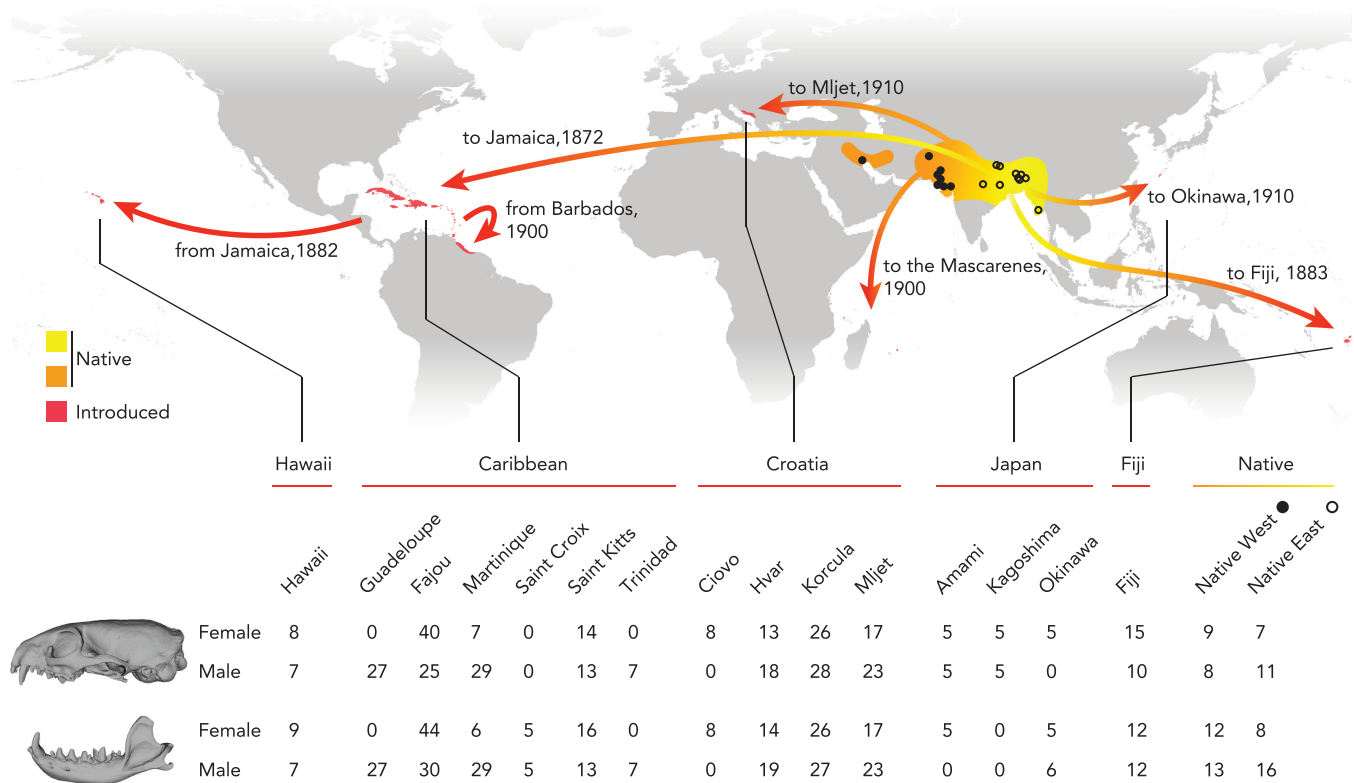

	Hawaii	Guadeloupe	Fajou	Martinique	Saint Croix	Saint Kitts	Trinidad	Ciovo	Hvar	Korcula	Mljet	Amami	Kagoshima	Okinawa	Fiji	Native West ●	Native East ○
Female	8	0	40	7	0	14	0	8	13	26	17	5	5	5	15	9	7
Male	7	27	25	29	0	13	7	0	18	28	23	5	5	0	10	8	11
Female	9	0	44	6	5	16	0	8	14	26	17	5	0	5	12	12	8
Male	7	27	30	29	5	13	7	0	19	27	23	0	0	6	12	13	16

Figure 1. Geographical distribution and introduction history of the small Indian mongoose populations sampled in this study.

in islands where the small Indian mongoose faces no competition. However, the conclusions of Barun *et al.* (2015) are not strongly supported because of partially contrasted results. In fact, the small Indian mongoose has also been introduced into one Adriatic island where the marten is not present. No difference was observed between this population and populations from other Adriatic islands, where the mongoose lives in sympatry with the marten, thereby contradicting the hypothesis of character displacement and character release.

In this study, we aim to investigate the impact of introduction to a novel biogeographical range on the pattern of morphological variation in the small Indian mongoose. More specifically, we are contrasting native and introduced populations in order to test for character displacement and character release, using head size and shape (cranium and mandible). This work includes populations from five islands that have never been sampled in previous studies (Guadeloupe, Martinique, St. Kitts, Kagoshima, and Okinawa). Concordantly with previous research, head shape and size were expected to vary between the introduced and native populations, with the skull being larger in introduced populations than in the native range, suggesting character release in response to the specific ecosystem structure of insular environments.

METHODS

Sample and data collection

Our dataset included 450 adult specimens of the small Indian mongoose from 23 islands and countries (Fig. 1; Supporting Information, Table S1). Specimens were loaned by the following institutions: the Muséum National d'Histoire Naturelle (MNHN, Paris, France), the Department of Mammalogy—American Museum of Natural History (New York, USA), the Florida Museum of Natural History (Gainesville, USA), the Field Museum of Natural History (Chicago, USA), the Hrvatski Prirodoslovni Muzej (Zagreb, Croatia), the Institut National de la Recherche Agronomique (INRA, Rennes, France), the Museum of Vertebrate Zoology (Berkeley, USA), the Natural History Museum (NHM, London, UK), the Office National de la Chasse et de la Faune Sauvage (ONCFS, France), the Office National des Forêts (ONF, France), Ross University School of Veterinary Medicine (St. Kitts), and the Department of Mammalogy, National Museum of Nature and Science (Japan). Among the 450 specimens, 422 were digitalized using a 3D surface scanner (Breuckmann SmartSCAN, AICON 3D Systems) at the MNHN, and 28 specimens were digitalized using a Nikon Metrology HMX ST 225 CT scanner at the CT facility of the NHM.

Geometric morphometrics

A total of 45 landmarks and 15 curves (semi-landmarks) were recorded on the surfaces of the crania, as well as 20 landmarks and 12 curves on the surfaces of the mandibles (Supporting Information, Tables S2, S3; Fig. S1). All landmarks were manually recorded by the same person (V.L.) using the software Stratovan Checkpoint v.2022.07.21.1321 (Stratovan Corporation). The curve semi-landmarks generated from Stratovan Checkpoint were resampled, and slid along curves in order to minimize

bending energy using the function «slider3d» from the package Morpho v.2.7 (Schlager 2017) implemented in the software R v.3.6.2 (R Development Core Team 2019). Generalized Procrustes superimpositions were realized using the function «gpagen» from the R package geomorph v.4.0.5 (Collyer *et al.* 2018, Baken *et al.* 2021, Adams *et al.* 2022, Collyer and Adams 2022).

Testing character displacement and character release hypothesis

If character release in response to changes in ecosystem composition occurs in introduced areas, we expect that introduced populations will have larger heads than native ones (i.e. a convergent trait with sympatric larger congeneric and other small carnivorans in the native range). Therefore, we investigated size variation between the various geographical origins of the specimens. Specimens from the native range were sorted in two geographical groups: individuals originating from the western part of the native range (Afghanistan, Iran, and Pakistan), and individuals originating from the eastern part (India, Nepal, and Myanmar) (Fig. 1). This separation appears coherent with the discontinuous distribution of sampled specimens, but also regarding ecosystem and environmental characteristics, with the western part of the native range being more arid and warmer than the eastern part.

Moreover, since the small Indian mongoose presents significant sexual dimorphism, we performed all analyses separately for each sex.

Centroid size values were log10-transformed to meet assumptions of normality and homoscedasticity. Difference in centroid size among the different geographical origins of the specimens was investigated using permutational univariate analyses of variance (ANOVAs), with 10 000 permutations, using the functions «procD.lm» of the R package geomorph v.4.0.5 (Collyer *et al.* 2018, Baken *et al.* 2021, Adams *et al.* 2022, Collyer and Adams 2022). Significance of pairwise comparisons of mean samples was assessed using the function «pairwise» of the R package geomorph v.4.0.5 (Collyer *et al.* 2018, Baken *et al.* 2021, Adams *et al.* 2022, Collyer and Adams 2022).

Testing the difference in head shape between populations

We investigated variation in allometric patterns among the different populations using multivariate analyses of covariance (MANCOVAs), with shape as the dependent variable, geographical origin as factor and centroid size as covariate. MANCOVAs were performed using the functions «procD.lm» of the R package geomorph v.4.0.5 (Collyer *et al.* 2018, Baken *et al.* 2021, Adams *et al.* 2022, Collyer and Adams 2022). Linear discriminant analyses (LDA) were performed using the R package MASS v.7.3-57, in order to visualize which populations differed significantly from the others.

To explore variation in shape of the cranium and mandible, we performed a principal component analysis (PCA) on the variance–covariance matrix of the Procrustes coordinates of all specimens. Shape visualizations along the principal components (PC) axes were realized using the R package Morpho v.2.7 (Schlager 2017) and rgl v.0.100.30 (Adler and Murdoch 2020). Scores of the PC that together explained more than 95% of the

overall shape variation (females: $N = 74$ for the crania, $N = 56$ for the mandibles; males: $N = 79$ for the crania, $N = 60$ for the mandibles) were used as new shape variables in further analyses in order to reduce the dimensionality of the dataset.

Investigating head shape structuration between and among populations

To further explore differences in shape among and between populations, we performed two pattern-recognition procedures: the k-nearest neighbours' algorithm (k-NN) and discriminant analyses of principal components (DAPC) (Jombart *et al.* 2010). The use of several algorithms, calling in different statistical procedures, makes it possible to identify congruent trends. The k-NN algorithm is a method of classification that allows assignment of an object to a group, using its k-NN by Euclidian distances (Ripley 1996). Here, we used this approach to assess the assignment of shapes (i.e. PC scores) to geographical origins. To determine the most appropriate values of k, we calculated the proportion of correct classifications for values of k varying from 1 to 30 using a cross-validation procedure, with 70% of the dataset as training data. k-NN analyses were performed using the core functions implemented in the software R v.3.6.2 (R Development Core Team 2019). The DAPC approach is a multivariate method designed to identify and describe structure in populations without a priori grouping (Jombart *et al.* 2010). Within the DAPC, variables (i.e. the variance–covariance matrix of the Procrustes coordinates) are first transformed using a PCA and subsequently groups are identified using discriminant analysis (DA). The number of groups (K) was identified through a K-means procedure. The optimal number of PCs was selected using a cross-validation method with 1000 replicates using a training set of 90% of the data using the R package adegenet v.2.1.8 (Jombart 2008).

Finally, we assessed the disparity in shape (as the sum of variances) of the crania and mandibles between populations using the function «dispRity.per.group» from the R package dispRity v.1.3.5 (Guillerme 2018). Pairwise differences were assessed using Student's t-test of significance with a Bonferroni correction.

RESULTS

Differences in head size between populations

Results of the ANOVAs show significant differences in sizes of the crania and mandibles between native and introduced populations (cranium: $F_{female} = 9.63$, $P_{female} < 0.001$, $F_{male} = 9.4$, $P_{male} < 0.001$; mandible: $F_{female} = 10.03$, $P_{female} < 0.001$, $F_{male} = 14.02$, $P_{male} < 0.001$) (Fig. 2). Pairwise tests reveal that the size of females is significantly different between introduced populations and individuals from the western part of the native range, but no significant difference is observed between introduced populations and individuals from the eastern part of the native range (Supporting Information, Tables S4, S5). Comparable trends are observed in males, with few exceptions: cranium size appear significantly different between two Croatian populations (Hvar and Mljet) and individuals from the eastern part of the native range; crania of Kagoshima appear significantly different from all native populations; mandible size of individuals from St. Croix, Trinidad, and Fiji are significantly different

from all native populations. In addition, while crania and mandibles in Croatian populations appear significantly smaller than those of all other introduced populations, no significant difference is observed between Croatian populations, whether they live in sympatry with the beech marten or not.

Difference in head shape between populations

The first two PCs accounted for 23.5% of the variance in crania of both females and males for crania: 25.5% in females and 23.2% in males for mandibles (Supporting Information, Fig. S2, S3). The scatterplot shows a clear distinction in morphospace between Croatian and Caribbean populations, while other populations overlap greatly.

Results of the MANCOVAs indicate a significant interaction between the geographical origin and the centroid size on shape, with the exception of male mandibles (female and male crania: $P < 0.001$; female mandibles: $P < 0.1$; male mandibles: $P = 0.82$; Supporting Information, Table S6). Shape is significantly different between geographical origins for both sexes. The linear discriminant analyses highlight the significant differentiation of the populations from Croatia, Fajou, Fiji, Japan, and individuals from the western part of the native range, while the individuals from the eastern part of the native range, other Caribbean populations and Hawaii overlap substantially (Fig. 3). These results are congruent in both female and male crania and mandibles.

Head shape structuration among and between populations

The k-NN classifications showed that more accurate assignments were obtained with k values of, respectively, 8 and 6 for female and male crania, and 5 and 6 for female and male mandibles. Overall, best population assignments were obtained for individuals from Croatia, Fajou, Fiji, Hawaii, Japan, and individuals from the western part of the native range (Fig. 4).

DAPCs for crania and mandibles support 4 and 5 groups to describe shape variation in females and males, respectively (Fig. 5; Supporting Information, Fig. S4). The groups resulting from cranium and mandible assignments for females, particularly, distinguish Croatian and Fajou populations. In addition, individuals in the western and eastern parts of the native range are assigned to different groups. The same classifications are observed for crania and mandibles of males, with a distinction of individuals from Hvar amongst the Croatian populations.

Finally, populations in the native range showed higher disparity in cranial and mandible shape than introduced populations (Fig. 6; Supporting Information, Tables S7, S8). Differences in disparity in cranial and mandible shape between native and introduced populations appear significant for all populations in males. In females, differences in disparity in cranial and mandible shape between native and introduced populations are not significant between western native specimens and populations from Hvar, Mljet, Fajou, Martinique, St. Kitts, and Hawaii.

DISCUSSION

This study presents the first comparative analysis of the morphology of the cranium and mandible of the globally introduced small Indian mongoose, *Urva auropunctata*, using geometric morphometrics' approaches, including samples from both
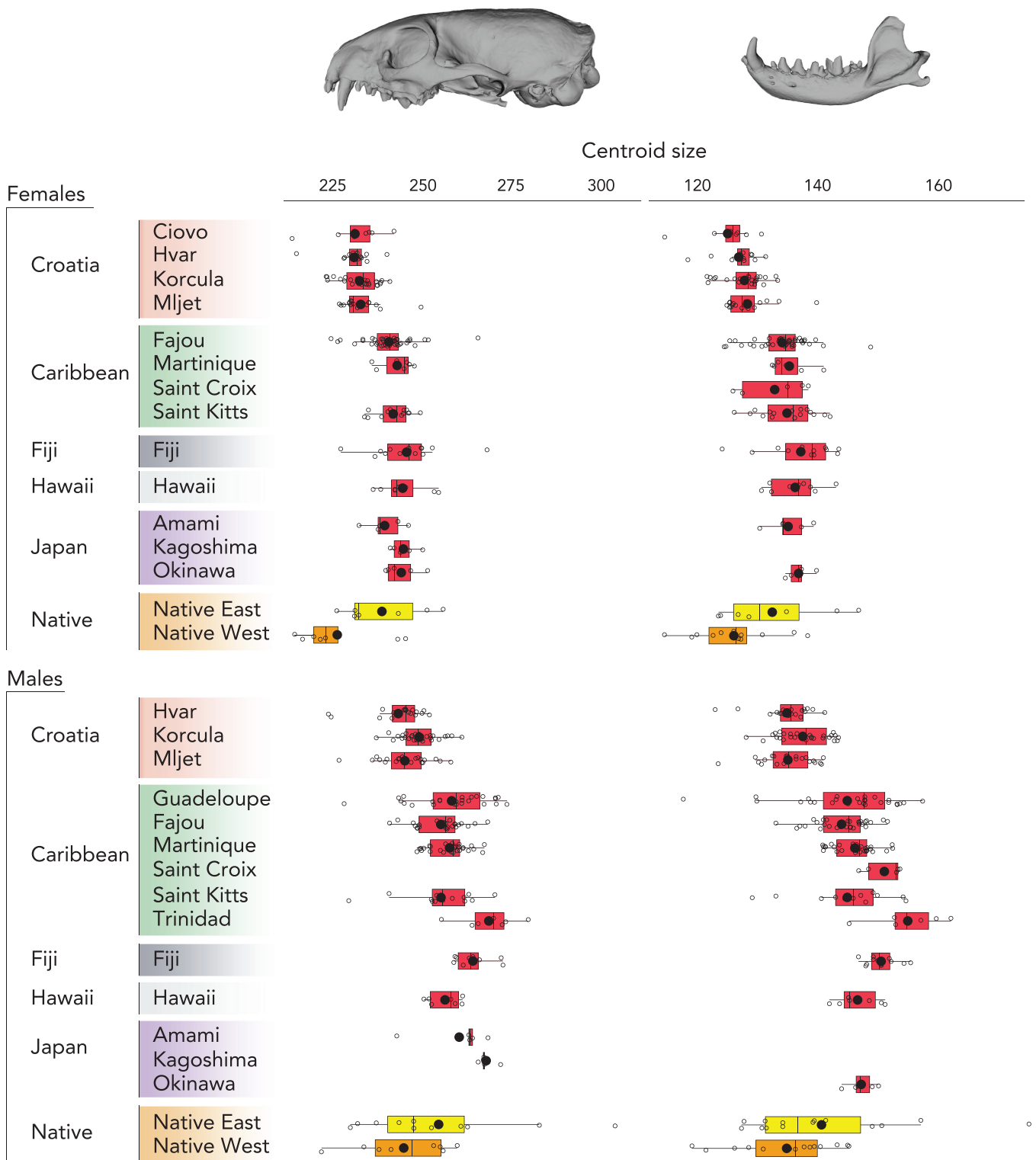
Figure 2. Centroid size of the crania and mandibles of the specimens of small Indian mongoose from sampled localities in the native and introduced range. Large circles indicate mean values.

native and introduced ranges. As expected, our results revealed significant differences in size and shape, of both the cranium and mandible between the various continental native and insular introduced populations. In addition, our analyses shed light on the relationships between these variations and the introduction history of the small Indian mongoose, which contradict previously proposed character displacement and character release hypothesis that were used to explain these variations.

Variation in head morphology and character release

Variation in size of an organism might be explained by changes in selection pressures associated with new environments, such
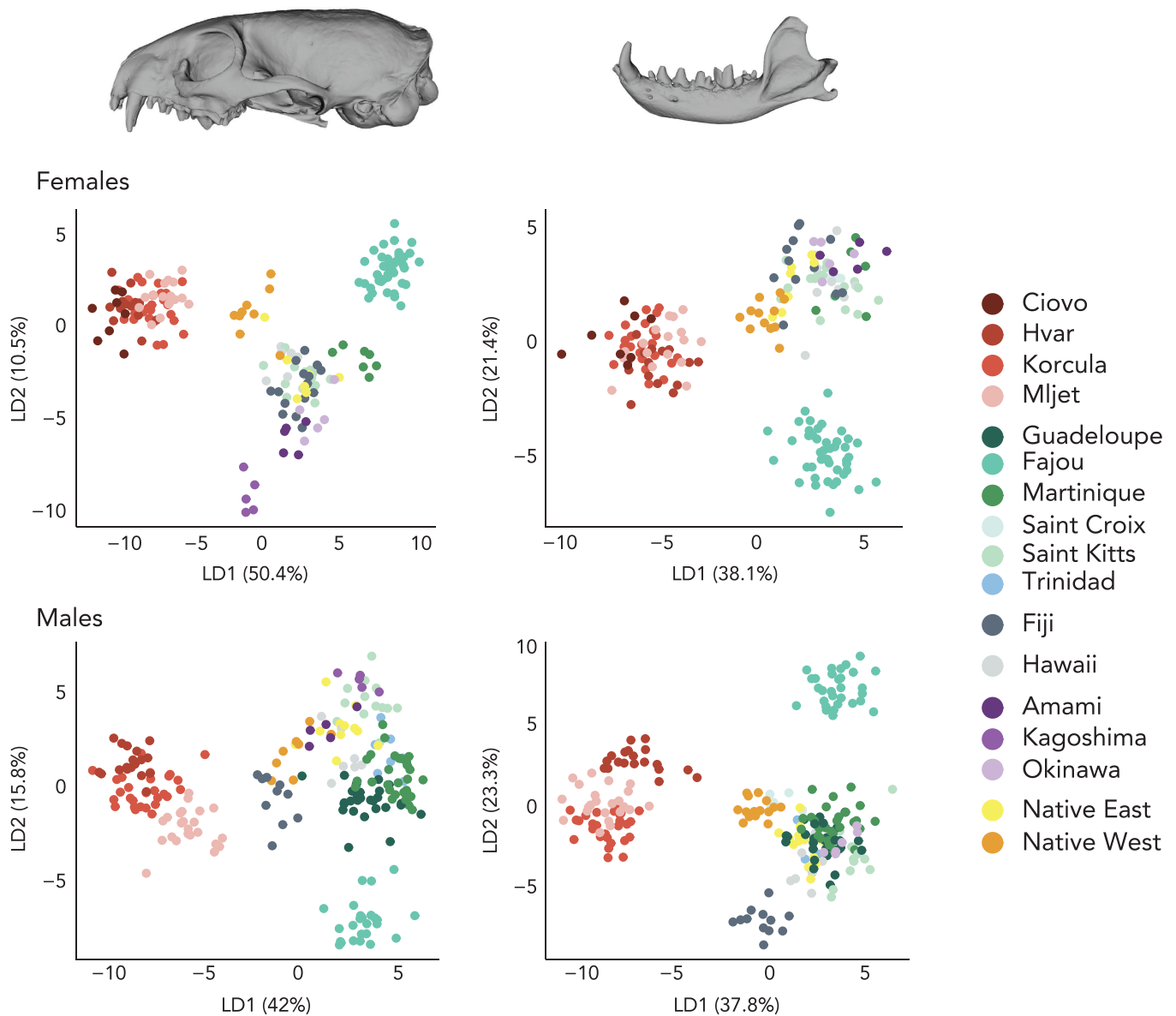
Figure 3. Linear discriminant analyses of cranial and mandibular shape from the sampled localities.

as niche widening, food availability, and release from competition. Increase in food availability was found to influence skull size in several mammal species (e.g. Patton and Brylski 1987, López-Fuster *et al.* 2000). Predator species, and particularly carnivorans, are poorly represented in insular ecosystems where the small Indian mongoose has been introduced. Consequently, the species faces little or no competition in these islands. This aspect, combined with higher number of naïve species in insular environments, might have promoted niche widening and increased food availability for the introduced populations of small Indian mongoose. Thus, Barun *et al.* (2015) proposed that the larger sizes observed in introduced populations of the small Indian mongoose might be reflecting character release in response to reduced competition pressure.

However, our results provide new insights into size variations observed in the small Indian mongoose. Interestingly, while introduced populations appear significantly larger than the individuals from the western region of the native range

(Afghanistan, Iran, Pakistan, and Kashmir), they do not appear significantly different in size from mongooses from the eastern part of the native range (India, Nepal, and Myanmar) (Fig. 2; Supporting Information, Tables S4, S5). In addition, and concordantly with Barun *et al.*'s (2015) results, Croatian specimens are significantly smaller than those from other introduced populations. However, no difference in size is observed among these populations whether they live in sympatry with the beech marten (which is the case in Hvar, Korcula, and Mljet) or not (as in Ciovo).

Shape also appears to be highly variable between the various introduced and native populations. Congruently with size variations, results from the LDA and the DAPC (Figs 3, 5) highlight the differences in shape between the two native populations, and the proximity between the eastern native individuals with Caribbean and Hawaiian populations, and slightly more contrasted with Fijian and Japanese populations. Moreover, all our analyses also consistently demonstrate the
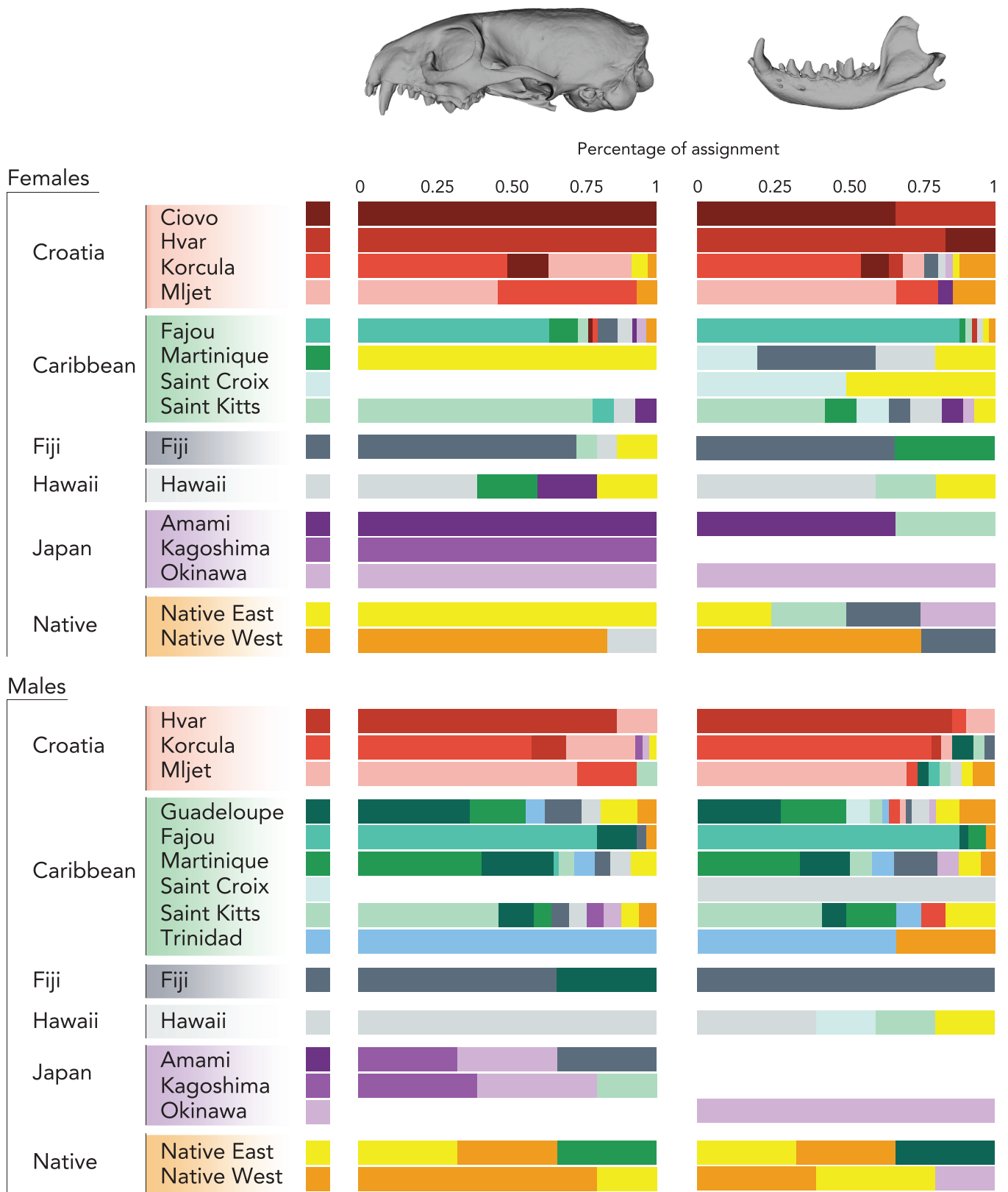
Figure 4. Cranial and mandibular shape assignments from the k-NN analyses.

distinctiveness of the head shape of Croatian populations, but once again, with no significant differences between Adriatic islands, where the mongoose and the marten co-occur, and those where they do not. Thus, our results contradict the hypothesis of character displacement and character release to explain size and shape variations observed in the skulls of different introduced and native populations of small Indian mongooses.
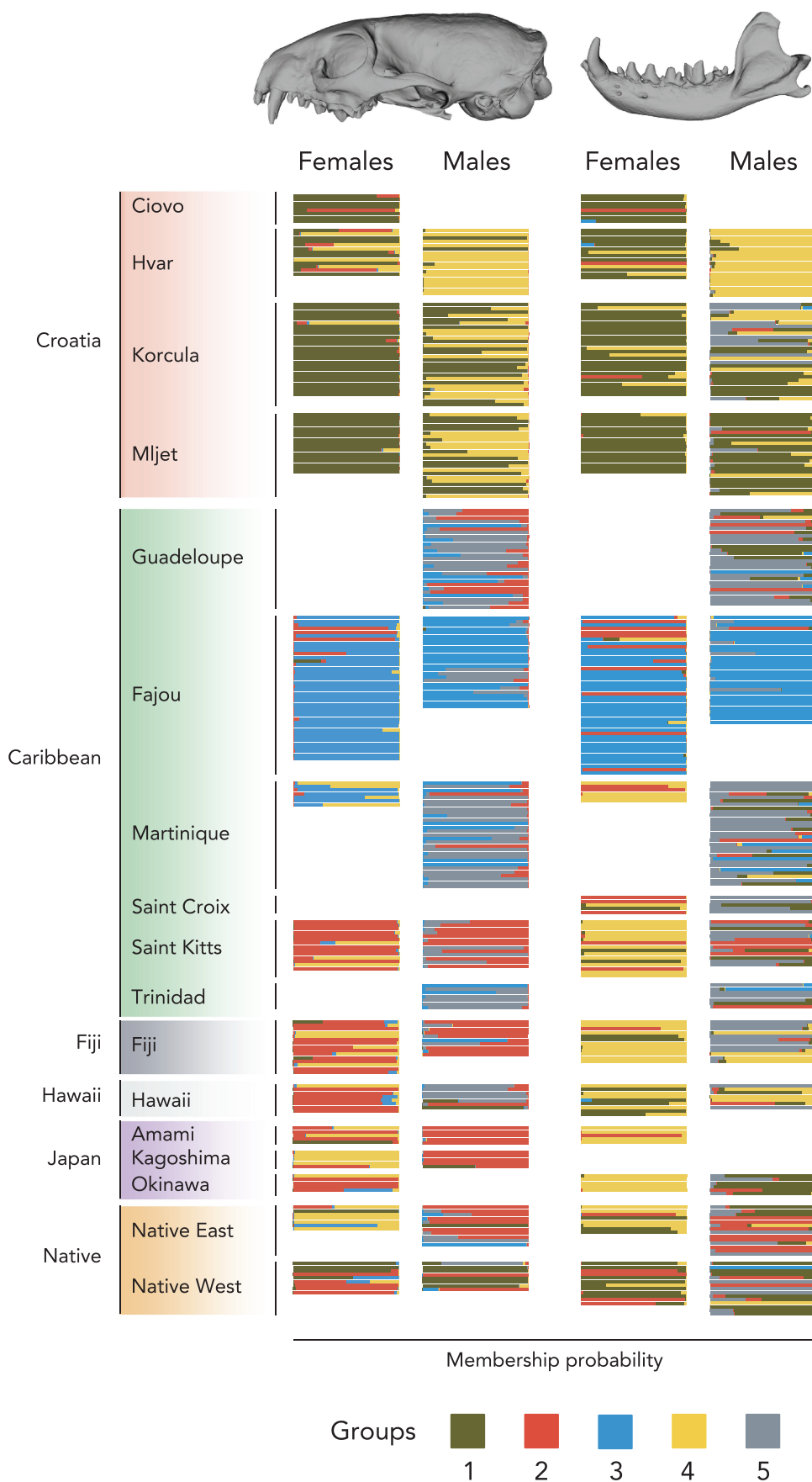
Figure 5. Cranial and mandibular shape assignments from the discriminant analyses of principal components.
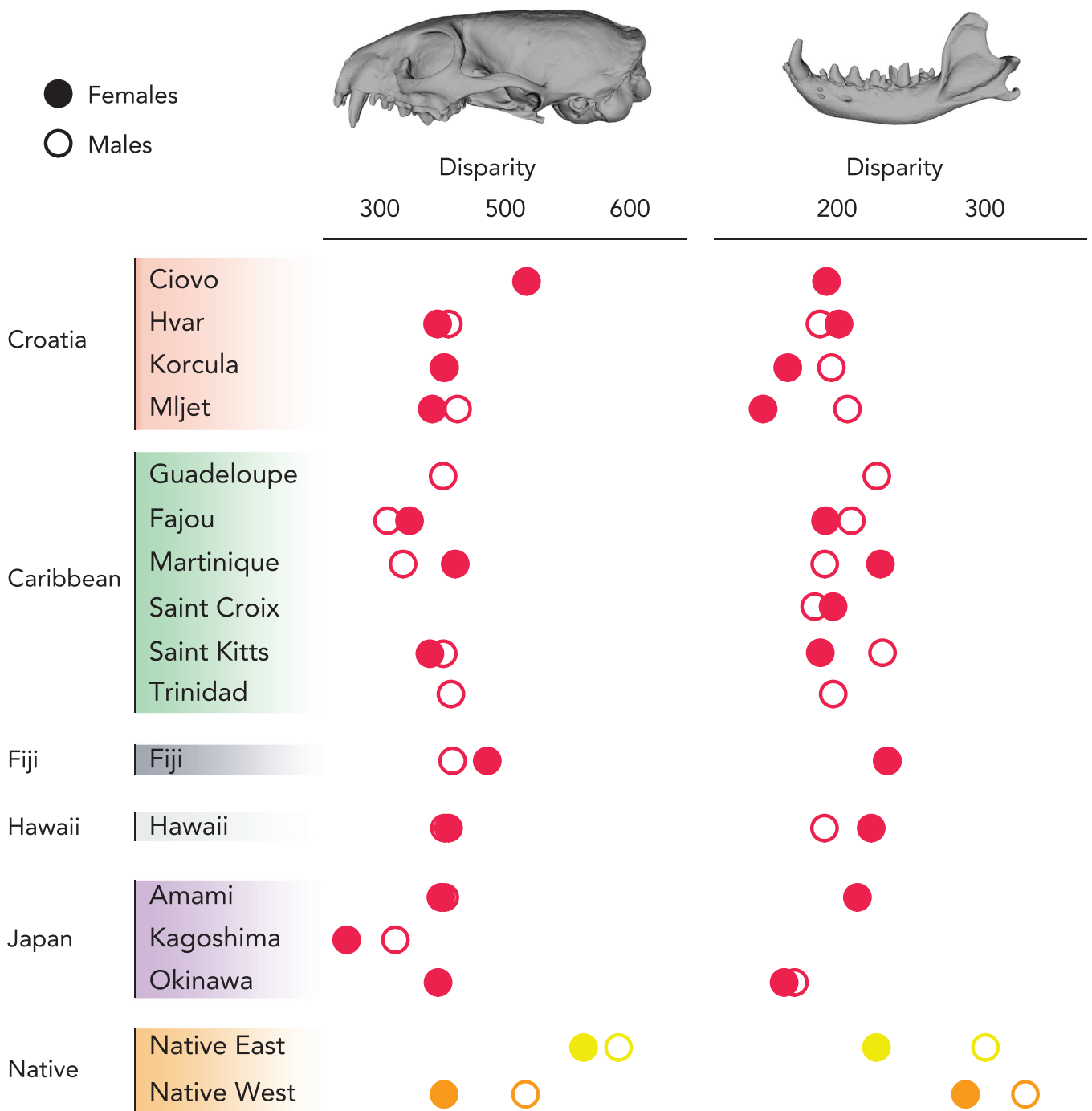
Figure 6. Disparity in cranial and mandibular shape.

Variation in head morphology through the prism of the introduction history

According to historical records and recent molecular genetic studies (Louppe *et al.* 2021b), the small Indian mongoose was introduced in the Caribbean, Fiji, and the Japanese archipelago from individuals most likely captured in the eastern part of the native range (in the vicinity of Calcutta and in Bangladesh; Fig. 1). The species was subsequently introduced from Jamaica to Hawaii. Despite the fact that the origin of several populations in the Caribbean remains to be clarified, our results appear congruent with the historical links between populations in the Caribbean, Hawaii, Fiji, and Japan, and the populations from the eastern region of the native range. On the other hand, the origin of the populations introduced in the Croatian islands remains unclear. According to historical records, several specimens have been introduced into Mljet in 1910 from India, and the species was subsequently introduced in other Adriatic islands, at least in part, from Mljet (Tvrtkovic and Krystufek 1990). At the time of the report, Pakistan was part of India. Interestingly, recent genetic results have shown the distinctiveness of specimens from Croatia and their closeness to specimens from Pakistan (Louppe *et al.* 2021b). Despite uncertainties, individuals introduced to

Croatian islands clearly originated from a different region than those introduced to the Caribbean, Hawaii, Fiji, and Japan. Thus, the distinctiveness of Croatian populations in terms of size and shape appears consistent with what is known of the introduction history of these populations. Ultimately, our results suggest that size and shape of the crania and mandibles of the introduced populations of small Indian mongoose have been little affected by changes in environmental conditions and ecosystem composition in areas to which they have been introduced.

Mosaic variations and patterns of microevolution

Our results show a significant interaction between shape and size differences among populations (Supporting Information, Table S6). This divergence in allometric trajectories, resulting in mosaic variations among populations, could reflect differences in ecological niche, habitat, and diet, but could also be related to microevolutionary processes. Founder effects and genetic drift, resulting from population bottlenecks created by human-mediated introduction events, can result in significant differentiation in size and shape, but also in reduced variation within a population (i.e. disparity). Introduced populations of small Indian mongoose were founded from few individuals (being native specimens or translocated from introduced regions) (Lorvelec *et al.* 2021, Louppe *et al.* 2021b). This might explain the mosaic variation and the reduced disparity observed in introduced populations, in comparison with native populations (Figs 4–6).

The population from Fajou clearly illustrates that introduced populations of small Indian mongoose are affected by the founder effect. Our results highlight the distinctiveness in shape of individuals from Fajou, and the low disparity within this population. The Îlet à Fajou (here Fajou) is a very small island (1.15 km²), in the Guadeloupean archipelago, which is located in the middle of the lagoon of the Grand Cul-de-Sac Marin, less than 5 km from the shores of the two main islands of Guadeloupe, Basse-Terre and Grande-Terre. The small Indian mongoose was intentionally introduced to Fajou in the 1930s from the main islands of Guadeloupe (Lorvelec *et al.* 2004, 2021), making this the most recent introduction in the Caribbean region. As demonstrated by the LDA and our pattern-recognition analyses, individuals from Fajou have cranial and mandibular shapes clearly different from those of all other populations, including Guadeloupe (Figs 3–5). Concordantly, recent molecular genetic studies, using microsatellite markers, have emphasized the genetic differentiation of the population of Fajou from the main and source islands of Guadeloupe (Louppe *et al.* 2021b). Our morphological results illustrate a founder effect, and confirm the high isolation of this population from those of the main islands of Guadeloupe, as suggested by the genetic structure (Louppe *et al.* 2021b) and the absence of re-colonization since the successful eradication of the species from Fajou in 2001 (Lorvelec *et al.* 2004).

CONCLUSION

Introductions of species outside their natural boundaries, whether intentional or accidental, represent unique case studies of intraspecific phenotypic variation. However, as illustrated in this study, an understanding of the introduction history of the species is essential in order to disentangle the mechanisms underpinning this variation. As such, our results demonstrate that the variations in head morphology of the small Indian mongoose across globally introduced populations reflect the intraspecific phenotypic variation observed in the native range. Thus, the mosaic variations mirror the introduction history of the species and the consecutive founder effects, rather than evolutionary or plastic processes resulting from changes in environmental conditions and ecosystems composition. Therefore, this low sensitivity to environmental and ecosystem changes in introduced regions could partly explain the ability of the small Indian mongoose to settle and disperse outside its natural boundaries. Further studies, including samples from key islands, such as Jamaica, as well as islands and native regions not sampled in this study, should be developed to ensure a better assessment of the morphological variability of the head of the small Indian mongoose. Moreover, differences in ecosystem composition and environmental characteristics might still influence morphological variability in the native range. Investigating concordant variations in other small carnivoran species will depend on our understanding of the factors driving phenotypic variation in the small Indian mongoose.

SUPPLEMENTARY DATA

Supplementary data are available at *Zoological Journal of the Linnean Society* Journal online.

AUTHOR CONTRIBUTIONS

V.L., A.-C.F., O.L., and G.V. conceived the study. V.L. and A.-C.F. designed the methodology. V.L. and A.-C.F. acquired the surface and

CT-scans. V.L. acquired the data, and V.L. and A.-C.F. interpreted the results. V.L. wrote the first draft of the manuscript, and all the authors contributed to its writing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

Upon acceptance, all data will be provided in the Dryad Digital Repository. The mesh data that support the findings of this study will be deposited in the Phenome10 K repository (http://phenome10k.org/) pending acceptance of the paper.

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