An integrated molecular and ecological trait dataset for the Tuscan Archipelago butterflies: a resource to understand the evolution and extinction of island biodiversity

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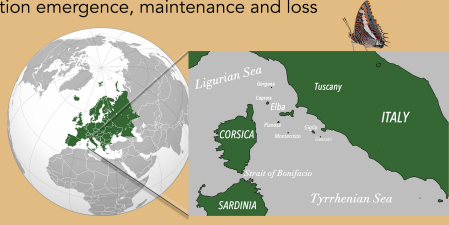
What?
Characterize species diversity in an island system and infer the species traits that are associated with diversification emergence, maintenance and loss

Who?
The butterfly communities

Where?
The Tuscan Archipelago, Corsica, Sardinia, Tuscany

Methods

- We carried out surveys in the study area, during the last 15 years, and gathered occurrence data from the literature of the last 115 years

- We sequenced the COI gene for 1303 specimens, representing the 46 butterfly taxa reported in the Tuscan Archipelago, including comparative material from Sardinia, Corsica and Tuscany

- We calculated the Dst and Gst to measure the genetic differentiation among populations, and we also estimated island haplotype uniqueness

- We assessed 12 species traits related to: feeding (the number of host plants), morphology (wingspan), life history (voltinism, length of flying period), physiology (mean annual temperature and precipitation)

- We evaluated the relationships between the different species traits and population diversification, using stepwise phylogenetic regressions

- We assessed the traits that could have influenced species extinctions on Elba and Capraia

Results

- We identified the species that probably became extinct or strongly declined on these islands: five on Elba, three on Giglio and six on Capraia (Table 1)

- Gst values had an almost bimodal distribution: 10 species with Gst<0.25 and 9 species with Gst>0.75 (Table 1, Figure 2)

- All three indices (Dst, Gst and Uni) showed that, together with the endemics, several common and widespread species provided a large contribution to diversity (Table 1)

- The phylogenetic regressions showed that small-sized, more generalist species that are occurring in drier areas have a higher genetic structure and/or haplotype uniqueness (Table 2)

	Trait variables	Estimate	StdErr	t.value	p.value
Gst	Host Plants	-0.1	0.045	-2.226	0.032
	Mobility PC1	-0.141	0.046	-3.031	0.004
	PhenologyPC1	0.058	0.043	1.363	0.181
	EcophysioIPC	0.068	0.04	1.713	0.095
Dst	Host Plants	-0.11	0.043	-2.55	0.015
	MobilityPC1	-0.126	0.047	-2.66	0.011
	PhenologyPC1	0.06	0.042	1.454	0.153
	EcophysioIPC	0.119	0.039	3.042	0.004
Uni	Host Plants	-0.045	0.028	-1.643	0.108
	EcophysioIPC	0.102	0.033	3.112	0.003

Table 2. Trait variables that entered the AIC phylogenetic regressions for Gst, Dst and Uni

- The overall spatial pattern of genetic variation corresponded to the proximity of the areas, but we identified strong contrasts between geographically close areas (Figure 3)

Species	Gst	Dst	Uni	Dis
Lasiommata megera/paramegaera	0.966	0.615	0.37	
Coenonympha corinna	0.943	2.194	0.19	G
Aglais urticae/ichnusa	0.937	0.449	NA	E
Pararge aegeria	0.88	0.636	0.076	
Hipparchia neomiris	0.871	0.968	End	C
Coenonympha pamphilus	0.864	0.86	0.152	
Callophrys rubi	0.846	0.279	0	
Carcharodus alceae	0.779	0.258	0.095	
Lycaena phlaeas	0.762	0.098	0.051	C
Aricia agestis/cramera	0.738	0.984	0.094	G
Iphiclides podalirius	0.701	0.063	0	
Plebejus bellieri/idas	0.616	0.134	0.051	
Maniola jurtina	0.603	0.298	0.085	C
Leptidea sinapis	0.501	0.081	0	E
Melitaea nevadensis	0.455	0.492	0.988	
Thymelicus acteon	0.432	0.067	0	
Pieris napi	0.432	0.133	0	
Issoria lathonia	0.431	0.014	0	
Spialia sertorius	0.417	0.009	0	
Nymphalis polychloros	0.415	0.043	NA	E
Favonius quercus	0.393	0.053	0.051	
Gonepteryx cleopatra	0.385	0.004	0	
Melitaea cinxia	0.379	0.54	NA	E
Melitaea didyma	0.344	0.07	0	
Gonepteryx rhamni	0.323	0.237	NA	E
Leptosia pirithous	0.298	0.048	0	
Zerynthia cassandra	0.293	0.053	0.152	
Hipparchia statilinus	0.281	0.053	0	
Pyronia tithonus	0.26	0.015	0	
Pyronia cecilia	0.26	0.224	0.091	C
Polyommatus icarus	0.216	0.018	0.076	G
Limenitis reducta	0.185	0.015	0	
Argynnis pandora	0.171	0.15	0.076	
Vanessa atalanta	0.127	0.009	0.051	
Hipparchia aristaeus	0.119	0.019	End	C
Pieris rapae	0.118	0.05	0.054	
Celastrina argiolus	0.114	0.011	0.076	
Pontia edusa	0.079	0.015	0.051	C
Lampides boeticus	0.044	0.005	0.038	
Vanessa cardui	0.032	0.007	0.038	
Charaxes jasius	0	0	0	
Glaucopsyche alexis	0	0	0	
Pieris mannii	0	0	0	
Papilio machaon	0	0	0.038	
Anthocharis cardamines	0	0	0.051	
Pieris brassicae	0	0	0.076	

Table 1. Species ranked for Gst, Dst and Uni. Dis, species that disappeared from Elba (E), Giglio (G) and Capraia (C)
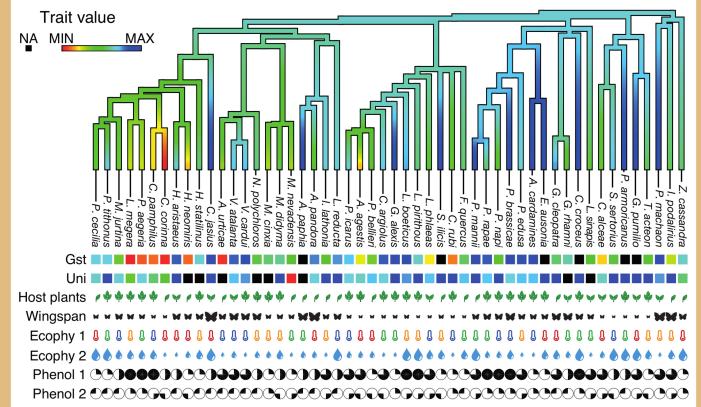
Results

Figure 2. Phylogenetic tree based on cytochrome c oxidase subunit 1 (COI) sequences of the butterfly fauna occurring in the Tuscan Archipelago, with their Gst, Dst, Uni and traits. The values of Dst are superimposed on the tree, while the square-root values for Gst and Uni are represented by different colors from the RGB scale. Black sectors of Phenol1 and 2 represent the time frame of the flight period (the top sector corresponds to January). Host plants represent the number of plant genera on which the larva of a given species has been reported: one leaf - one genus; two leaves two to four genera, three leaves more than four genera. The size of the butterfly silhouettes is directly correlated with the species size (wingspan). The icons for Ecophy1 and 2 represent mean values of the annual temperature and precipitation that each species experiences where it occurs. Ecophy 1 is illustrated by a blue (low residuals) to red (high residuals) scale, while Ecophy2 is represented by the dimension of the drops.
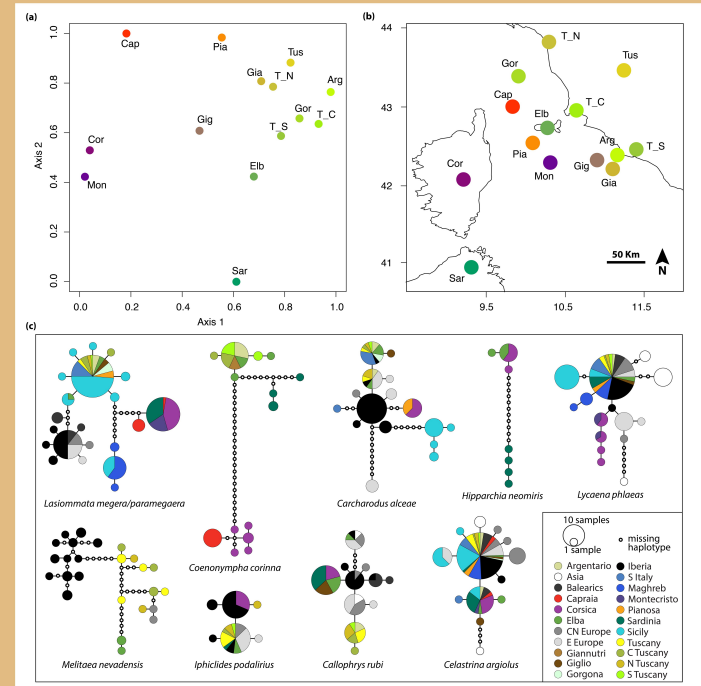

Figure 3. Overall genetic patterns obtained after comparisons among islands, based on Gst. (a) The colours obtained in the RGB projection of the Principal Coordinate Analyses (PCoA) have been included in (b) the map of the studied region to show similarity and contrast among areas. Locality codes are: Arg, Argentario; Cap, Capraia; Cor, Corsica; Elb, Elba; Gia, Giannutri; Gig, Giglio; Gor, Gorgona; Mon, Montecristo; Pia, Pianosa; Sar, Sardinia; Tus, Tuscany; T_C, central Tuscany coast; T_N, northern Tuscany coast; T_S, southern Tuscany coast. (c) Haplotype networks based on COI for nine particularly interesting species, obtained by comparing haplotypes from the study area with other regions of Europe.

Conclusions

There was a considerable degree of population diversification in many species, which confirms that the Tuscan Archipelago hosts highly diverse butterfly communities. Phylogenetic regressions showed that smaller-sized and more specialized species, with a preference for drier regions, display greater genetic structure and/or uniqueness. Moreover, species adapted to colder and wetter areas and with shorter flight periods are more likely to become extinct.
The methodology used here can be applied to reveal fine-scale diversity patterns, their origins and the vulnerability of taxa to current and future environmental changes, thus providing a valuable tool for evidence-based conservation prioritization.