Biochemical Systematics and Ecology 37 (2009) 341–348

Contents lists available at ScienceDirect

Biochemical Systematics and Ecology

journal homepage: www.elsevier.com/locate/biochemsyseco

The relationships between cuticular hydrocarbon composition, faunal assemblages, inter-island distance, and population genetic variation in Tuscan Archipelago wasps

Leonardo Dapporto[a,b], Aviva E. Liebert[c,*], Philip T. Starks[c], Stefano Turillazzi[a,b]

[a] *Dipartimento di Biologia Animale e Genetica, Università di Firenze, via Romana no 17, 50125 Florence, Italy*
[b] *Centro Interdipartimentale di Spettrometria di Massa, Università di Firenze, Viale G. Pieraccini no 6, 50100 Florence, Italy*
[c] *Department of Biology, Tufts University, 163 Packard Avenue, Medford, MA 02155, USA*

ARTICLE INFO

Article history:
Received 7 October 2008
Accepted 30 May 2009

Keywords:
Island biogeography
Pompilidae
Polistes dominulus
Tuscan Archipelago
Cuticular hydrocarbons
Genetic differentiation

ABSTRACT

Until recently, studies examining the geographical distribution of insects in the Tuscan Archipelago have focused on paleogeography as the primary influence on species distributions. However, for flying insects such as Hymenoptera that may be able to disperse over water, current geographical location is likely to be more important in determining present distributions within the Archipelago. Here we compare mainland and island wasp populations using genetic variation and cuticular hydrocarbon composition of the vespid wasp *Polistes dominulus*, and species composition of wasps in the family Pompilidae. Both chemical and genetic data result in similar clustering of *P. dominulus* populations that reflect present geographical location. Moreover, we found current geographical distance to be significantly correlated with *P. dominulus* population genetic differentiation and Pompilidae faunal composition. These data suggest that dispersal over present sea distances is more important in determining population differentiation and species distribution in the Tuscan Archipelago than paleogeography.

1. Introduction

In the last two centuries much effort has been spent investigating how living and fossil animals could have reached their geographical distribution. Generally two hypotheses have been considered as opponents in determining species distribution: the vicariance and the dispersal hypotheses. The former predicts that a species becomes separated into two populations by some newly emerged barrier and the populations then diverge in different areas, while the latter predicts that a species evolves and spreads from a center of origin until it reaches some physical or ecological barrier (Williamson, 1981; Whittaker, 1998). Due to the possibility of supporting the continental drift hypothesis and predicting or explaining species distribution on the basis of continental movement, the vicariance model has received the majority of attention. Nevertheless evidence from recent studies suggests that the distribution of highly mobile organisms on continental islands (e.g., those in the Mediterranean Sea) can be explained best by recent geography rather than paleogeography (Dennis et al., 2000; Hausdorf and Hennig, 2005; Dapporto et al., 2007a; Dapporto and Cini, 2007; Dapporto and Dennis, 2008). The assessment of similarity

---

[*] Corresponding author. Present address: Department of Biology, Framingham State College, 100 State Street, Framingham, MA 01701-9101, USA. Tel.: +1 508 626 4790; fax: +1 508 626 4794.

E-mail addresses: leondap@gmail.com (L. Dapporto), aliebert@framingham.edu (A.E. Liebert), philip.starks@tufts.edu (P.T. Starks), stefano.turillazzi@unifi.it (S. Turillazzi).

0305-1978/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.bse.2009.05.018

patterns among biota of different areas, and thus implicitly their current and past relationships, may be revealed by using several techniques. The most widely used are i) the comparison of whole faunal assemblages and ii) the analysis of similarities among populations of few or single selected taxa based on morphological and genetic traits (Whittaker, 1998; Humphries and Parenti, 1999; Gillespie, 2004; Hausdorf and Hennig, 2005; Heaney, 2007; Schmitt, 2007; Dapporto and Dennis, 2009).

Recently, Dapporto et al. (2004) utilized a different character to study biogeographic patterns. They used as a comparative character the highly informative cuticular hydrocarbon (CHC) composition of different populations of *Polistes dominulus* to study the biogeographical patterns of the Tuscan Archipelago. The complex cuticular blend of this species is affected by both genetic and environmental factors (Singer et al., 1998; Dani et al., 2004; Dani, 2006; Dapporto et al., 2007b). Cuticular hydrocarbons may thus give information about the relationships among populations and about a large spectra of environmental factors in the considered areas (substrate, climate, floral and prey composition). A combined examination of genetic variability and CHCs among island populations would help determine the relative importance of habitat and heritability in determining the composition of cuticular lipids and reinforce its reliability as a tool for testing biogeographical hypotheses. In this paper we compare variation in allele frequencies, CHC composition of *P. dominulus* populations, and faunistic composition of Pompilidae wasps, in order to determine if historical or contemporary factors influenced the distribution of wasps among islands, and thus the composition of their CHCs.

2. Methods

2.1. Study area

Tuscan Archipelago consists of seven main islands ranging in size from Gorgona (2.2 km^2) to Elba (223.5 km^2) (Fig. 1). The islands have different lithology and geological origins. Gorgona is characterized by two different metamorphic units (sedimentary and ophiolitic). The volcanic island of Capraia originated approximately nine million years ago, after a series of eruptions. Montecristo is a plutonic granite massif about seven million years old (Borsi et al., 1967), as is almost the entire Giglio Island. Elba is mountainous in its western part, with the granite massif of Mt. Capanne (the highest peak of the Archipelago, 1018 m), whereas in the eastern part, gneiss and marble emerge; the plains of the central area, densely populated, are alluvial made up of clay, sandstone, and limestone. The origin of Pianosa is different again: it consists of sedimentary rocks and shell formations.

The climate of the Tuscan Archipelago is typically Mediterranean. The climax vegetation type was probably the oak (*Quercus ilex*) forests, which are now drastically reduced in scattered patches. The present-day dominant vegetation types throughout the islands are Mediterranean shrubs, garigue, and anthropic landscape and vegetation.

Fig. 1. The studied area. Monte Nerone, not included in the map, is located about 160 Km North-East of Venturina.

2.2. Sample collection

We collected 89 females of *P. dominulus* from different localities, all at sea level and within two kilometers of the coast on Corsica Island (La Marana, $n = 14$; Bacugnana, $n = 10$), Elba Island (Procchio, $n = 2$, Capoliveri, $n = 2$), Giglio Island (Castello, $n = 10$), Capraia Island (Isola, $n = 8$), Pianosa Island ($n = 7$), Gorgona Island ($n = 15$) and Tuscany (Venturina, $n = 7$) (Uccellina, $n = 4$), (Monte Nerone, $n = 6$). All these localities share similar environmental characteristics (Mediterranean bushes).

In order to limit the influence of parameters such as colony, sex, rank, and caste, we collected flying females from the second half of June to the end of July 2003. In this species it is not easy to distinguish nest-founding females (foundresses) from workers, but catching flying females in the restricted period ensures a high probability of collecting only workers.

2.3. Chemical sampling

Chemical data were obtained from a subset of the collected samples: Corsica Island (La Marana, $n = 3$; Bacugnana, $n = 2$), Elba Island (Procchio, $n = 2$, Capoliveri, $n = 2$), Giglio Island (Castello, $n = 5$), Pianosa Island ($n = 6$), Gorgona Island ($n = 5$), Capraia Island ($n = 6$), (Venturina, $n = 5$), (Uccellina, $n = 4$). Peak areas of the epicuticular gas-chromatogram of each wasp were transformed into percentages of the total CHCs. We calculated a dissimilarity matrix among the cuticular profiles of the wasps using squared Euclidian distances (*Z*-scores were used to standardize the percentages). To visualize the pattern of proximity between wasp chemical profiles we used a cluster analysis (Ward's method). We also calculated a dissimilarity matrix among the localities for which we had data on CHCs, genetics, and Pompilidae fauna (Corsica, Capraia, Gorgona, Elba, Giglio, Pianosa, and Uccellina in the Tuscan mainland), by calculating the mean dissimilarity among all the possible wasp pairs for each pair of localities. We sampled CHCs using a method similar to that described by Turillazzi et al. (1998). A piece of filter paper was gently rubbed on the wasp's thoracic scutum for 30 s using sterile forceps. Thereafter, the filter paper was placed in an aluminum sheet and then in a sterile vial. The epicuticular compounds were later extracted from the filter paper in 300 µl of pentane for 10 min. The solution was then dried in a nitrogen stream and re-eluted in 25 µl of heptane for GC–MS analysis. We injected 2 µl of solution into a Hewlett Packard (Palo Alto, CA) 5890A gas chromatograph coupled with an HP 5971A mass selective detector. A fused silica capillary column coated with 5% diphenyl–95% dimethyl polysiloxane (Rtx-5MS, 30 m × 0.25 mm × 0.5 µm; Restek, Bellefonte, PA) was used in the GC analysis. The injector port and transfer line were set at 280 °C and the carrier gas was helium (at 12 psi). The temperature protocol was: 70–150 °C at a rate of 30 °C/min (held for 5 min), and 150–310 °C at 5 °C/min (held for 11.3 min). Analyses were performed in splitless mode. Identification of cuticular compounds was performed on the basis of their mass spectra produced by electron impact ionisation (70 eV).

2.4. Microsatellite genotyping

After CHC sampling, individual wasps were shipped in 70–100% ethanol to the International Social Insect Research Facility at Tufts University, Medford, Massachusetts, USA where they were stored at −80 °C until further analysis. Microsatellite genotyping protocols were the same as in Liebert et al. (2006). We isolated genomic DNA from two legs per wasp by grinding the frozen tissue with sterile minipestles (Strassmann et al., 1996), then incubating the samples in 250 µl of a 5% Chelex® solution (Crozier et al., 1999, modified slightly from Walsh et al., 1991). We then amplified the DNA of each wasp at six microsatellite loci using primers developed for this species (Henshaw, 2000: Pdom1CAG, Pdom2AAG, Pdom25AAG, Pdom122AAT, Pdom127bAAT, and Pdom140TAG; Table 1). Finally, alleles were visualized on 6.5% denaturing polyacrylamide gels using a LI-COR single channel 4200 NEN Global Edition IR^2 DNA Analyzer and scored with SAGA^{GT} 2.1 software.

2.5. Genetic data analysis

The computer program Genepop on the Web (Raymond and Rousset, 1995: http://genepop.curtin.edu.au) was used first to confirm that the allele frequencies of each population were consistent with expectations for Hardy–Weinberg equilibrium, to test for linkage disequilibrium, and to calculate FST, a measure of genetic differentiation between populations. The program MicroChecker (Van Oosterhout et al., 2004: http://www.microchecker.hull.ac.uk) was used to check for evidence of null alleles and large allele dropout. We then used four programs within the PHYLIP analysis package (Felsenstein, 2005) to generate a consensus neighbor-joining tree of the sampled populations based on their microsatellite allele frequencies. To do

Table 1
Microsatellite loci used for genetic analysis.

Locus	Total no. of alleles	Mean expected % heterozygotes
Pdom1CAG	9	0.572
Pdom2AAG	7	0.544
Pdom25AAG	7	0.623
Pdom122AAT	28	0.824
Pdom127bAAT	20	0.846
Pdom140TAG	18	0.744

this we first used the program SEQBOOT to generate 1000 replicate datasets using the bootstrapping method, and then used GENDIST to calculate genetic distances (Cavalli-Sforza's chord distance) between all the replicate populations. To generate a tree, we first used the program NEIGHBOR to create neighbor-joining trees from the previously generated distance data, and then used CONSENSE to build a consensus tree. Branch lengths were specified according to the PHYLIP documentation files by using the program FITCH with computed distances between populations as input data. Finally, the program TreeIllustrator Version 0.5 (Trooskens et al., 2005; http://nexus.ugent.be/geert/index.php) was used to draw the resulting tree.

2.6. Geographic distance calculation

We compiled a matrix incorporating the shortest over water distances connecting each pair of localities. The choice to use over water distances instead of direct distances is due to the fact that animals typically disperse faster through the land compared to sea (Hausdorf and Hennig, 2005).

The possible correlations among the four matrices created as described above (Chemical dissimilarity, genetic differentiation, Pompilidae faunal similarity, and geographic distance) were assessed with a Mantel test using Matman 1.0 program (we used 1000 permutations and Spearman Rho).

3. Results

For the chemical analysis, we detected a total of 35 peaks representing one or more compounds. The chemical composition reflects the results of Dapporto et al. (2004). Cluster analysis, performed on the percentages of compound peak areas, separated chemical profiles into two distinct blocks. The first block included Elba, Giglio, Pianosa, Uccellina and Venturina cuticular signatures, while the second block included Corsica, Capraia, and Gorgona. Except for Giglio wasps, within each block individuals from the same locality did not cluster together and, consequently, no well-defined subgroups emerged (Fig. 2).

Genetic analysis showed a very similar pattern. Wasps from Corsica clustered together with wasps from Gorgona and Capraia in 910 of 1000 trees, while the other islands showed a greater similarity with Italian mainland wasps (Fig. 3; Table 2). Mantel test results showed a correlation between CHC dissimilarity and genetic differentiation (FST) matrices among populations (Spearman $\text{Rho}_{\text{rw}} = 0.437$, $P = 0.036$). CHC dissimilarity was also correlated to Pompilidae fauna similarity obtained

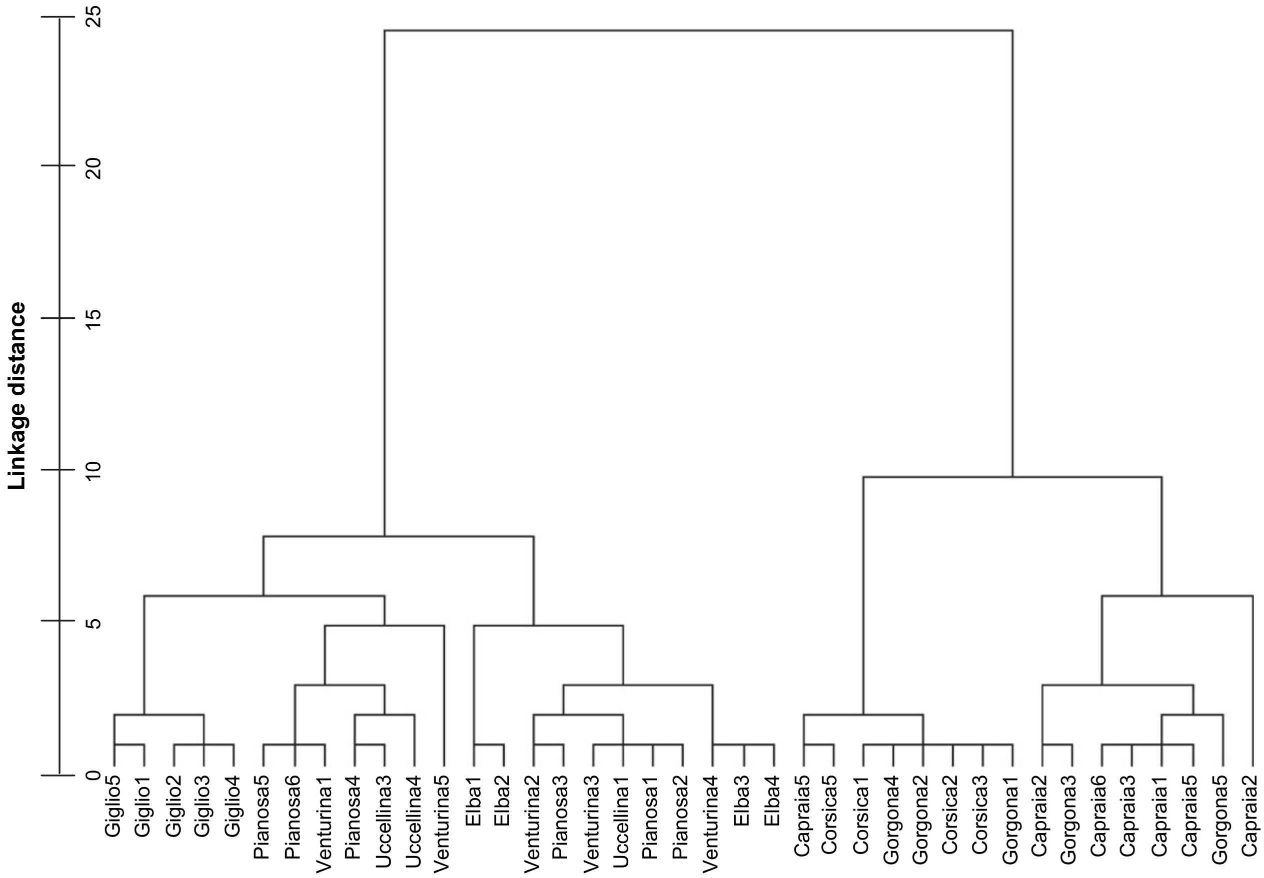

Fig. 2. Cluster analysis of the individuals from the different localities.

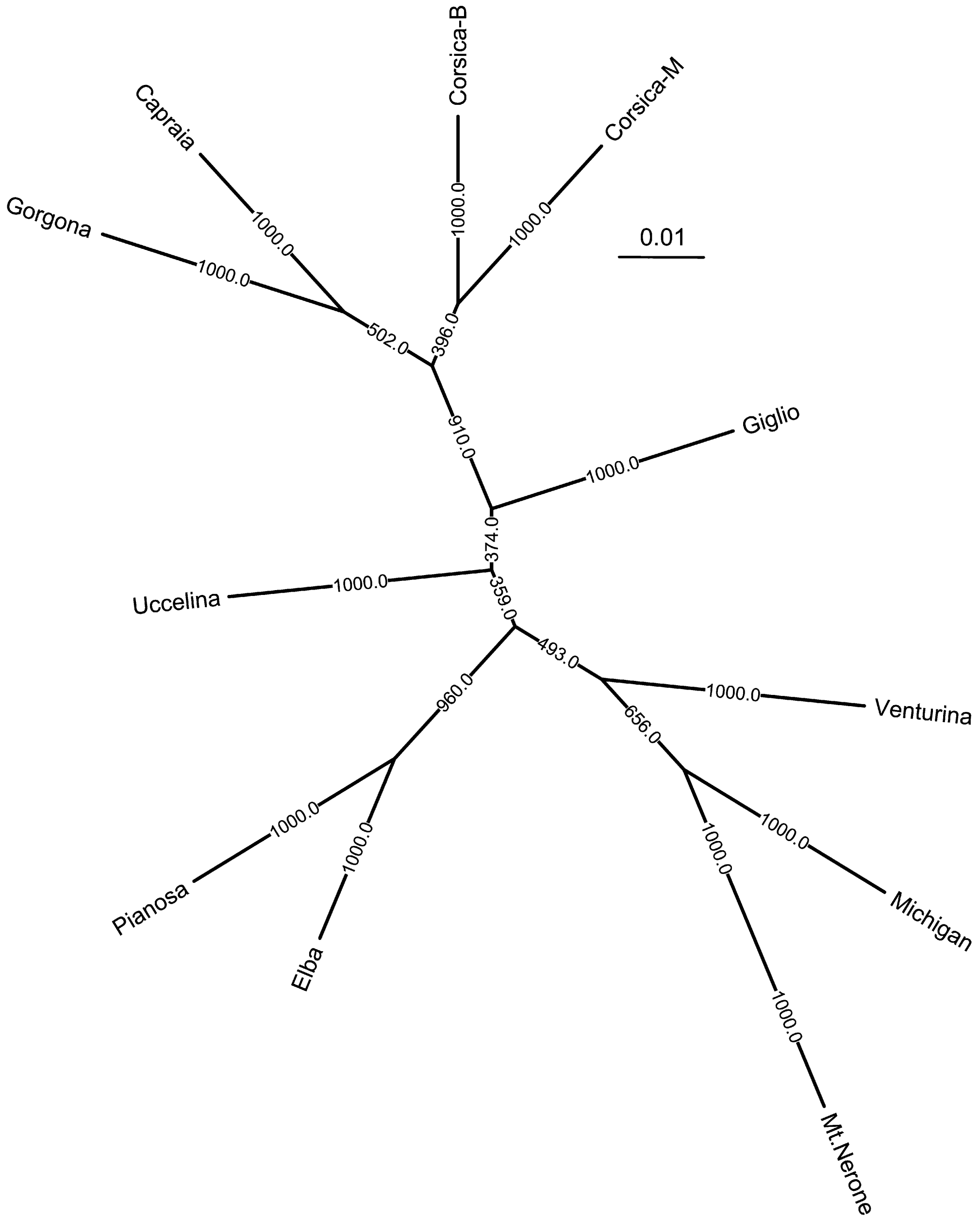

Fig. 3. Consensus tree based on genetic distances between eight populations, generated from 1000 bootstrapped datasets of allele frequencies at six microsatellite loci. A population from Michigan, U.S.A. was used as the outgroup; Corsica-B and Corsica-M refer to Bacugnana and La Marana, respectively. Numbers refer to the number of trees out of 1000 in which that particular division of populations occurred, and the scale bar indicates a genetic distance of 0.01.

by Dapporto et al. (2007a,b) (Spearman $\text{Rho}_{\text{rw}} = -0.425$, $P = 0.029$) but not geographic distance (Spearman $\text{Rho}_{\text{rw}} = 0.273$, $P = 0.119$). Conversely, genetic differentiation was related to geographic distance (Spearman $\text{Rho}_{\text{rw}} = 0.430$, $P = 0.026$; Fig. 4) but not to Pompilidae fauna similarity (Spearman $\text{Rho}_{\text{rw}} = -0.294$, $P = 0.08$). Finally, Pompilidae fauna similarity was revealed to be related to geographic distance (Spearman $\text{Rho}_{\text{rw}} = -0.425$, $P = 0.029$).

Table 2
Genetic differentiation (FST) values between populations.

	Corsica-B	Corsica-M	Capraia	Giglio	Gorgona	Elba	Pianosa	Uccelina
Corsica-M	0.0172							
Capraia	0.1427	0.0026						
Giglio	0.1505	0.2216	0.2994					
Gorgona	0.1671	0.1327	0.1017	0.296				
Elba	0.0591	0.0376	0.0534	0.0062	0.1231			
Pianosa	0.0486	0.1121	0.3254	0.1398	0.2962	0.0897		
Uccelina	0.0403	0.0887	0.2535	0.1387	0.2369	0.0652	−0.043	
Venturina	0.1144	0.1866	0.2523	−0.043	0.2394	−0.1018	0.0807	0.0073

4. Discussion

The Tuscan Archipelago is located in the Mediterranean Sea between Corsica (a large island separated from the European continent during the Miocene) and the Italian Peninsula. Due to its position this Archipelago contains standard transitional fauna and flora between Corsica and Italy. Consequently, many studies have been carried out in this Archipelago with the goals of i) searching for Corsica and Sardinia endemics and ii) explaining the present distribution of animals and plants. Until now most of these studies have focused on demonstrating support for the idea that paleogeographic events from the Miocene to the Pleistocene sea regression were responsible for the present pattern of distribution not only of animals with limited dispersal ability, but also of flying insects (Società Italiana di Biogeografia, 1974; Jutzeler et al., 1996; Ketmaier et al., 2003; Strumia, 2003).

Recently, several studies have re-evaluated the importance of dispersal in shaping animal distribution in this area, especially for the case of flying insects. Specifically, Dapporto et al. (2007a), Dapporto and Cini (2007), Dapporto and Dennis (2008), Fattorini (2009) demonstrated that present-day determinants shape butterfly and Hymenoptera richness and composition in the Italian islets as well as in the Tuscan Archipelago. Accordingly, our data suggest that current sea distances between Tuscan Archipelago populations, and therefore dispersal ability, is largely responsible for the *P. dominulus* genetic variation and Pompilidae species composition. This is clearly demonstrated by the Mantel tests showing significant genetic isolation by geographical distance for *P. dominulus* (Fig. 4) and the significant correlation of Pompilidae species composition and geographical distance. Interestingly, the clustering of populations into two main blocks (Capraia–Corsica–Gorgona and Pianosa–Elba–Giglio–mainland Tuscany) is found in three different kinds of analyses: allele frequencies (Fig. 3), CHC composition (Fig. 2), and faunal similarity in Pompilidae species (Dapporto et al., 2007a). The influence of contemporary distances in determining species assemblages has been recently demonstrated in some flying solitary insects in the Mediterranean (Pompilidae and Chrysididae wasps: Dapporto et al., 2007a; Fattorini, 2009; butterflies: Dennis et al., 2000; Hausdorf and Hennig, 2005; Dapporto and Cini, 2007; Dapporto and Dennis, 2008; Fattorini, 2009). However, compared to Pompilidae, Chrysididae and butterflies, *Polistes* wasps should be less prone to dispersal. Indeed it has been clearly demonstrated that foundresses of this species (reproductive individuals) are highly philopatric and tend to remain in the natal sites to hibernate and found new colonies (Strassmann, 1983; Starks, 2003; Dapporto and Palagi, 2006).

Recent studies also demonstrated in Sardinia, Corsica and Tuscan Archipelago that ecological parameters different from distances and paleogeography are important determinants in shaping distributions mainly of the taxa with very low vagility (Ketmaier et al., 2003, 2005; Dapporto and Cini, 2007; Dapporto and Dennis, 2009; Fattorini, 2009). In particular, genetic studies have been used to verify historical and/or contemporary influences in biogeography and systematics. For the Western Mediterranean several studies have used genetic data to verify the rotation of Sardo–Corsican plate (Caccone et al., 1994; Ketmaier et al., 2003, 2005). This is the first attempt to verify the pattern of genetic similarity in this area by using a flying species.

It is interesting to note that similarities among islands in Pompilidae fauna composition and *P. dominulus* genetic differentiation between islands are not correlated as expected if geographical contemporary factors are the sole determinants of these characteristics. This may be explained in part by the fact that arrival on islands is only the prerequisite for a species to colonize an island (Williamson, 1981; Whittaker, 1998). A variety of factors, such as microclimate, substrate, specific food requirements (prey, host plants), and competition with established species, may determine success or failure of colonization (Whittaker, 1998). The correlation between genetic variation and CHC profiles of *P. dominulus* wasps also provides support for a heritable component to CHC composition, but the lack of a strong correlation between CHC dissimilarity and geographical distance also emphasizes the importance of environmental influences on chemical composition. Wasps feed on a wide variety

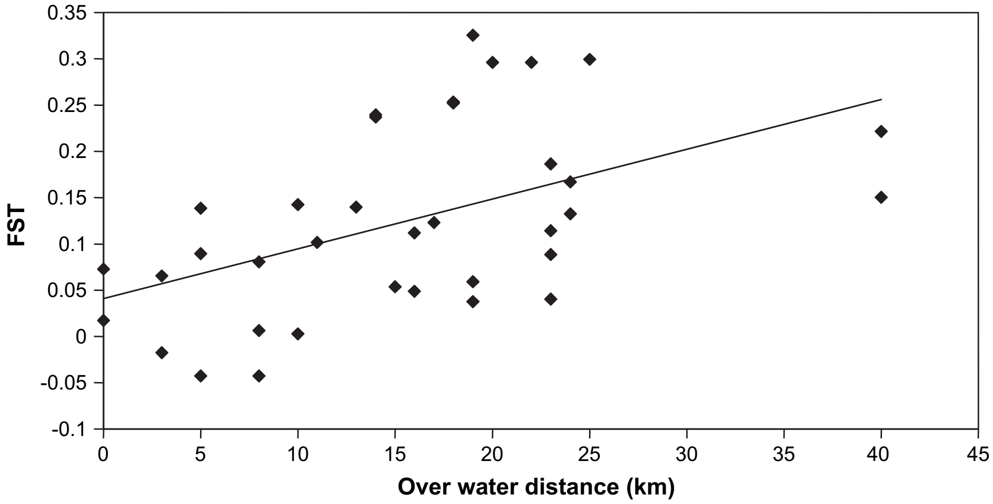

Fig. 4. Relationship between genetic differentiation among populations (FST) and geographic (over water) distance. Mantel test of increasing isolation by distance, [one-tailed p-value = 0.026 (based on 10000 permutations using Matman 1.0].

of prey and plants. It has been demonstrated that insect cuticular hydrocarbons depend not only on genetic components but also on food (Liang and Silverman, 2000). Several plants and insects on which wasps feed may have different determinants for distribution in Tuscan Archipelago depending of their vagility and habitat requirements (Dapporto and Cini, 2007; Fattorini, 2009). Intriguingly, CHCs showed the same pattern of similarity as the genetic and faunistic data, each of which encompasses diverse sources of information (gene flow, environmental characteristics, and historical influences). In this respect our data seem to confirm the hypothesis made by Dapporto et al. (2004) stating that CHCs should be considered as a sort of *trait-d'union* between genetic traits and environmental variables. Our results reinforce the idea that CHCs could represent a rapid and valuable tool to emphasize biogeographical patterns of similarity based both on gene flow and environmental characteristics.

Acknowledgements

This study was conducted in collaboration with the Tuscan archipelago National Park. We also wish to thank the director and personnel of Gorgona prison for allowing us to study butterflies on the island, and the "Stazione Forestale di Follonica" for making it possible to conduct research on Montecristo. The research was financed by a grant from the European INTERREG II-III project.

We also thank an anonymous referee for improving the manuscript and Matthew Sullivan for help with the microsatellite genotyping.

References

Borsi, S., Ferrara, G., Tongiorgi, E., 1967. Determinazione con il metodo K-Ar della età delle rocce magmatiche della Toscana. Boll. Soc. Geol. It 86, 403–410.

Caccone, A., Milinkovitch, M.C., Sbordoni, V., Powell, J.R., 1994. Molecular biogeography: using Corsica–Sardinia microplate disjunction to calibrate mitochondrial rDNA evolutionary rates in mountain newts (*Euproctus*). J. Evol. Biol. 7, 227–245.

Crozier, R.H., Kaufmann, B., Carew, M.E., Crozier, Y.C., 1999. Mutability of microsatellites developed for the ant *Camponotus consobrinus*. Mol. Ecol. 8, 271–276.

Dani, F.R., 2006. Cuticular lipids as semiochemicals in paper wasps and other social insects. Ann. Zool. Fenn. 43, 500–514.

Dani, F., Foster, K.R., Zacchi, F., Seppä, P., Massolo, A., Carelli, A., Arévalo, E., Queller, D.C., Strassmann, J.E., Turillazzi, S., 2004. Can cuticular lipids provide sufficient information for colony nepotism in wasps? Proc. R. Soc. Lond., B 271, 745–753.

Dapporto, L., Palagi, E., Turillazzi, S., 2004. Cuticular hydrocarbons of *Polistes dominulus* as a biogeographic tool: a study of populations from the Tuscan Archipelago and surrounding areas. J. Chem. Ecol. 30, 2139–2151.

Dapporto, L., Wolf, H., Strumia, F., 2007a. Recent geography determines the distribution of some flying Hymenoptera in the Tuscan Archipelago. J. Zool. (Lond.) 272, 37–44.

Dapporto, L., Dani, F.R., Turillazzi, S., 2007b. Social dominance molds cuticular and egg chemical blends in a paper wasp. Curr. Biol. 17, r504–r505.

Dapporto, L., Palagi, E., 2006. Wasps in the shadow: looking at the pre-hibernating clusters of *Polistes dominulus*. Ann. Zool. Fenn. 43, 583–594.

Dapporto, L., Cini, A., 2007. Faunal patterns in Tuscan archipelago butterflies: the dominant influence is recent geography not paleogeography. Eur. J. Entomol. 104, 497–503.

Dapporto, L., Dennis, R.L.H., 2008. Species' richness, rarity and endemicity of Italian offshore islands: complementary signals from island-focused and species-focused analyses. J. Biogeogr. 35, 664–674.

Dapporto, L., Dennis, R.L.H., 2009. Conservation biogeography of large Mediterranean islands. Butterfly impoverishment, conservation priorities and inferences for an ecological island paradigm. Ecography 32, 169–179.

Dennis, R.L.H., Shreeve, T.G., Olivier, A., Coutsis, J.G., 2000. Contemporary geography dominates butterfly diversity gradients within the Aegean archipelago (Lepidoptera: Papilionoidea, Hesperioidea). J. Biogeogr. 27, 1365–1383.

Fattorini, S., 2009. Both recent and Pleistocene geography determines animal distributional patterns in the Tuscan Archipelago. J. Zool. 277, 291–301.

Felsenstein, J., 2005. PHYLIP (Phylogeny Inference Package) Version 3.6. Distributed by the Author. Department of Genome Sciences, University of Washington, Seattle.

Gillespie, R., 2004. Community assembly through adaptive radiation in Hawaiian spiders. Science 303, 356–359.

Hausdorf, B., Hennig, C., 2005. The influences of recent geography, paleogeography and climate in the composition of the fauna of the central Aegean islands. Biol. J. Linn. Soc. 84, 785–795.

Heaney, L.R., 2007. Is a new paradigm emerging for oceanic island biogeography? J. Biogeog. 34, 753–757.

Henshaw, M.T., 2000. Microsatellite loci for the social wasp *Polistes dominulus* and their application in other polistine wasps. Mol. Ecol. 9, 2155–2234.

Humphries, C.J., Parenti, L.R., 1999. Cladistic Biogeography, second ed. Oxford University Press, Oxford.

Jutzeler, D., Biermann, H., de Bros, E., 1996. Elevage de *Coenonympha corinna elbana* (Staudinger, 1901) du Monte Argentario (Toscano, Italie) avec explication géologique de l'aire de repartition de complex *corinna* (Lepidoptera: Nymphalidae, Satyrinae). Linn. Belg. 15, 332–347.

Ketmaier, V., Argano, R., Caccone, A., 2003. Phylogeography and molecular rates of subterranean aquatic Stenasellid Isopods with a peri-Tyrrhenian distribution. Mol. Ecol. 12, 547–555.

Ketmaier, V., Giusti, F., Caccone, A., 2005. Molecular phylogeny and historical biogeography of the land snail genus *Solatopupa* (Pulmonata) in the peri-Tyrrhenian area. Molec. Phylogenet. Evol. 39, 439–451.

Liang, D., Silverman, J., 2000. You are what you eat: diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*. Naturwissenschaften 87, 412–416.

Liebert, A.E., Gamboa, G.J., Stamp, N.E., Curtis, T.R., Monnet, K.M., Turillazzi, S., Starks, P.T., 2006. Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. Ann. Zool. Fenn. 43, 595–624.

Raymond, M., Rousset, F., 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Hered. 86, 248–249.

Schmitt, T., 2007. Molecular biogeography of europe: pleistocene cycles and postglacial trends. Front. Zool. 4, 11.

Singer, T.L., Espelie, K.E., Gamboa, G.J., 1998. Nest and nestmate discrimination in independent-founding paper wasps. In: Vander Meer, R.K., Breed, M.D., Winston, M.L., Espelie, K.E. (Eds.), Pheromone Communication in Social Insects. Westview Press, Oxford.

Società Italiana di Biogeografia, 1974. Il popolamento animale e vegetale dell'Arcipelago toscano. Lavori della Società Italiana di Biogeografia 5.

Starks, P.T., 2003. Natal nest discrimination in the paper wasp, *Polistes dominulus*. Ann. Zool. Fenn. 40, 53–60.

Strassmann, J.E., 1983. Nest fidelity and group size among foundresses of *Polistes annularis* (Hymenoptera: Vespidae). J. Kans. Entomol. Soc. 54, 621–634.

Strassmann, J.E., Solís, C.R., Peters, J.M., Queller, D.C., 1996. Strategies for finding and using highly polymorphic DNA microsatellite loci for studies of genetic relatedness and pedigrees. In: Ferraris, J., Palumbi, S.R. (Eds.), Molecular Zoology. Wiley, New York, pp. 163–180.

Strumia, F., 2003. New and rare *Hedychridium* species from Italy and Mediterranean islands (Hymenoptera, Chrysididae). Ital. J. Zool. 70, 191–198.

Trooskens, G., De Beule, D., Decouttere, F., Van Criekinge, W., 2005. Phylogenetic trees: visualizing, customizing and detecting incongruence. Bioinformatics 21, 3801–3802.

Turillazzi, S., Sledge, M.F., Moneti, G., 1998. Use of a simple method for sampling cuticular hydrocarbons from live social wasps. Ethol. Ecol. Evol. 10, 293–297.

Van Oosterhout, C., Hutchinson, W.F., Wills, D.P.M., Shipley, P., 2004. Micro-Checker: software for identifying and correcting genotyping errors in microsatellite data. Mol. Ecol. Notes 4, 535–538.

Walsh, S., Metzger, D.A., Higuchi, R., 1991. Chelex^R 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material. BioTechniques 10, 506–513.

Whittaker, R.J., 1998. Island Biogeography: Ecology, Evolution, and Conservation. Oxford University Press, Oxford.

Williamson, M.H., 1981. Island Populations. Oxford University Press, Oxford.