

Gene Flow by Selective Emigration as a Possible Cause for Personality Differences Between Small Islands and Mainland Populations

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Abstract: Whether personality differences exist between populations is a controversial question. Even though such differences can be measured, it is still not clear whether they are due to individual phenotypic responses to the environment or whether they have a genetic influence. In a population survey we compared the personality traits of inhabitants of an Italian archipelago (the three Egadi islands; $N = 622$) with those of the closest mainland population (Trapani area; $N = 106$) and we found that personality differences between small populations can be detected. Islanders scored significantly lower on the personality traits of openness to experience and extraversion and higher on conscientiousness. We suggest that these personality trait differences could be an adaptive response to a confined socio-environmental niche, genetically produced by a strong, non-random gene flow in the last 20–25 generations, rather than the flexible response of islanders to environmental variables. To test this hypothesis, we compared subsets of the islander population classified by ancestry, birthplace, immigration and emigration and found that differences in extraversion can be accounted for by gene flow, while openness to experience and conscientiousness can also be accounted for by some gene–environment interactions. We propose a Personality Gene Flow hypothesis suggesting that, in small isolated communities, whenever there is strong, non-random emigration, paired with weak and random immigration, we can expect rapid genetic personality change within the population. Copyright © 2010 John Wiley & Sons, Ltd.

Key words: personality traits; Big Five; Personality Gene Flow hypothesis; small islands

INTRODUCTION

Evidence for a genetic influence on personality reported in the scientific literature is often controversial (Crawford, 2007). Recently, heritability researchers have started to converge on an estimation of the genetic component in personality traits of between 30% and 60% (Benjamin, Li, Patterson, Greenberg, Murphy, & Hamer, 1996; Ebstein, Novick, Umansky, Priel, Osher, & Blaine, 1996; Jang, Livesley, Angleitner, Riemann, & Vernon, 2002; Turkheimer, D’Onofrio, Maes, & Eaves, 2005). Some studies have shown that specific genes are closely associated with specific traits (Benjamin, Ebstein, & Belmaker, 2002; Benjamin et al., 1996; Hansenne et al., 2002). Despite growing evidence, these findings are still debated, as in the case of DRD4 (Ebstein, 2006). Personality traits, which constitute a complex phenotype, are likely to be influenced by a number of interacting genes (Eley, Dale, Bishop, Price, & Plomin, 2001; Jang, McCrae, Angleitner, Riemann, & Livesley, 1998).

Many researchers highlight the role of gene–environment interactions in the study of personality at an individual level (O’Connor, Caspi, DeFries, & Plomin, 2003; Penke,

Denissen, & Miller, 2007a; Plomin & Crabbe, 2000; Plomin, Pedersen, Lichtenstein, & McClearn, 1994; Reiss, Neiderhiser, Hetherington, & Plomin, 2000; Turkheimer, 2000). However, differences of opinion still exist as to how and why there is so much variability of personality within populations, and little convincing evidence has been found of personality differences between populations that have different cultural and linguistic origins (Allik & McCrae, 2002; Allik & McCrae, 2004; Eysenck & Yanai, 1985). Terracciano, Abdel-Khalek, Adam, Adamovova, Ahn, and Ahn (2005), who analysed 3989 people from 49 different cultures, found that the perception of personality characteristics of one’s own and others’ cultures are based on unfounded stereotypes that may serve the function of maintaining national identity (Robins, 2005; Terracciano et al., 2005). Others suggest there is a resistance to recognizing genetically influenced population differences in behavioural traits. This has caused most people to regard admitting the existence of such differences as unacceptable (Crawford, 2007). Our position is that the possible genetic influence on personality traits in populations constitutes an interesting scientific discussion that should be approached with an open mind and a sound scientific approach. In order to assess personality differences between populations, Camperio Ciani et al. (Camperio Ciani, Capiluppi, Veronese, & Sartori, 2007; Camperio Ciani, & Ceccarini, 2002) used a

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new approach, initially developed to study sexual orientation (Camperio Ciani, Corna, & Capiluppi, 2004), consisting of comparing small isolated populations with a reference population which shares a common historical, linguistic and cultural context. In a population survey conducted in three Italian archipelagos they found significant differences between islander and mainlander personality traits on a Big Five scale (Costa & McCrae, 1992; Goldberg, 1990; McCrae & Costa, 1999) based on the adjectives questionnaire validated for Italian language (Perugini & Di Blas, 2002; Perugini & Leone, 1994; Piconi, 1998). The emerging islander personality profile was characterized by lower *extraversion* and *openness to experience*, and more *conscientiousness* and *emotional stability* than in the mainland inhabitants: they suggested these personality differences could represent traits which result in better adaptation to the island environment. Immigrants to the islands (who had been resident for at least 20 years) were significantly more *extraverted* and more *open to experience* than original islanders, that is they retained a mainlander profile despite long-lasting permanence in the insular environment, which led the authors to suspect the presence of a genetic influence on personality, however, the study could not definitely exclude that behaviours learned during childhood were retained in adulthood. Emigrant islanders were found to be more *open to experience* and more *extraverted* than sedentary islanders. Camperio Ciani et al. (2007) suggested gene flow as the possible genetic selection mechanism (Bodmer & Cavalli-Sforza, 1976; Camperio Ciani, Stanyon, Scheffrahn, & Sampurno, 1989), that is the voluntary emigration of fertile individuals who were, in this case, higher in *extraversion* and *openness to experience*.

The purpose of this study is firstly to assess whether the personality trait differences between islanders and mainlanders reported in Camperio Ciani et al. (2007; Camperio Ciani & Ceccarini, 2002) can be detected in a different archipelago with similar socio-ecological conditions to previously studied islands.

Hence, we try to answer the following three questions:

1. Are there differences in personality traits between islanders and mainlanders?
2. Can these differences be ascribed to stable traits of genetic origin, or are they due to individual flexible adaptation to the environment?
3. Which mechanism could account for the origin of these differences?

Van Oers proposed the 'founder effect' (Van Oers, 2007) as a further explanation of genetic mechanism to explain how these personality differences come about. The *founder effect* is by definition a chance effect (non-adaptive) (Bodmer & Cavalli-Sforza, 1976), hence if the same results can be found in a novel archipelago, this alternative hypothesis would be less likely.

A further alternative to the genetic explanation of the personality differences suggested by Camperio Ciani et al. is the influence of early experience. According to the Big Five paradigm, the first years of life might contribute to the shaping of the definitive personality profile (Costa & McCrae, 1992; McCrae & Costa, 1999). The role of the environment could

influence individuals through early experiences during infancy (Forgas & Van Heck, 1992), given that most immigrants lived their childhood on the mainland. To address this alternative *Early Experiences* hypothesis, we studied the immigrant subjects in greater depth. Finally, we discuss whether a general explanation for such a rapid and significant personality divergence in small isolated environments can be derived and then extended to similar contexts.

For each question we present arguments based on empirical evidence by comparing the relevant sample subsets of the population under investigation.

METHODS

Population under investigation

We selected the Egadi archipelago, the southernmost set of islands off the coast of western Sicily because it has similar linguistic and socio-ecological conditions to those of the previous study, and we had access to all the relevant historical and geographical details required to test our hypothesis.

The Egadi islands (Favignana, Levanzo and Marettimo and a few other islets) constitute the southernmost Italian archipelago, 15–30 sea miles off the western shore of Sicily where the town of Trapani is situated. The total population in the Egadi archipelago is at present 4394, of which 220 are resident in Levanzo Island, 450 in Marettimo Island and the rest in Favignana Island. Only 50% of those who are listed as resident are actually living on the island, the remaining 50% are listed as being resident but have, in fact, emigrated. These islands fulfil the requisites of the long-lasting isolation required to highlight the hypothesized effect of the adaptive selection for personality traits. Even if the archipelago is now a tourist destination, during the last 400 years these islands have experienced limited immigration, a fact confirmed by surname analysis and by studies of birth, marriage and death registries (Veronese, 2003). This means that for at least 20–25 generations the small village communities did not mix extensively with the mainland population.

In order to allow a detailed comparison with the study by Camperio Ciani et al. (2007), the same criteria were used to identify the specific control population. The population of the whole of Italy is not adequate because Italy is a highly fractioned country in terms of regional culture, dialects and traditions. To account for such variables the closest coastal land to the Egadi was selected as the control population, in the region of Trapani (Sicily), which shares the same culture, language and latitude. This control population, composed of people from both urban and rural areas, is defined as Mainlanders and is used as the reference group to which all other populations are compared. Naturally this control population has also its limits due to its limited geographic distribution and different history from the archipelago.

Historical account

Cave graffiti show that the Egadi Islands have been populated since the Paleolithic era and since then a multitude of

different populations have controlled the islands, all attracted by the island's strategic position in the Mediterranean. In the middle ages the archipelago was attacked, raided and invaded by the Normans, the Angioinis, the Sicilians and the Hispanics, so that no permanent population was able to survive. The Tunisian pirate Adir Kadir undertook in 1516 the last significant raid that depleted the whole population of the Egadi. After that last episode, no other large scale invasions occurred and, in the second half of 1500, the Spanish crown and the new owner, the Count Pallavicini, re-founded the Egadi population by forcing about 70 families to move to the archipelago from Liguria (homeland of the Pallavicini) and Sicily and Spain (Gallitto, 2008), giving them housing, permission to cultivate the islands and work in the tuna fish farms (Calleri, 2006). Most of the surnames of these founding families are still present in the island population as indicated in the parish records. Since that time no further significant immigration has occurred (Calleri, 2006; Gallitto, 2008; Veronese, 2003). Given that life on the islands was anything but attractive, the only source of immigration over the last 400 years was prisoners, exiled people (from all over Italy and North Africa) and their jail officers, which were sent to the renowned caved prisons on the two main islands of the archipelago, Favignana and Marettimo. This excluded the possibility of auto-selective immigration based on personality traits. (Calleri, 2006; Gallitto, 2008; The Italian Heritage, 2009; Veronese, 2003). Only well after 1960 did a new source of immigration arrive in the form of the new opportunities offered by tourism, which attracted businessmen and workers from the tourism industry.

Emigration, on the other hand, has been very high, over 30% for each generational cohort due to population growth and agricultural overexploitation (Calleri, 2006). Emigration was so high that in 1810 the Florio family, the new owners of the islands, was obliged to transfer three to four new families to work in the tuna fishing farms. Emigration continued due to the hard conditions on the islands. The rocky environment made agriculture extremely hard and tuna fishing began to decline as a result of the competition of other developing Mediterranean countries (Gallitto, 2008).

The historical accounts show that the population seldom exceeded 2000 inhabitants in the whole archipelago. In the last 400 years, fecundity, as documented in parish records, averaged between 5 and 7 children per woman, and infant mortality has never exceeded typical rates for Southern Italy (Calleri, 2006). The infant mortality rate averaged between 20% and 30% from the 16th to the 19th century, then progressively decreased to 1% in 1952 and 0.4% in 2009 (Italian National Statistic Institute: ISTAT, 2009). Despite high fecundity and relatively low mortality, the population did not grow because there was a continuous outflow of emigrants, which in the past century averaged about 35% of each generation. Most emigrants in the last century (the last four generations) went to California (Monterrey), Argentina, Australia and Northern Italy (The Italian Heritage, 2009). Some of them, in late age, returned to the archipelago and were sampled in this study.

Survey subjects

The study subjects were selected using systematic and snowball sampling (Kish, 1995), by a team of 18 trained volunteer assistants, who were unaware of the research hypotheses. The same selection procedure was used for both the island and the mainland sub-samples. Eight hundred and seventy-eight subjects were examined, 622 living on the three islands and 106 resident and born in Trapani; 150 subjects were excluded from the analysis because they lacked one or more of the inclusion prerequisites: that is having Sicilian origins and having a clearly identified ancestry (known parents and grandparents origin). In the sample, there are a number of related individuals due to the relatively small size of the total population and the relatively high rate of endogamy, given that our sample includes over 15% of the Egadi resident population. Particular effort was made to classifying all possible sub-groups of individuals living in the island, to be able to discriminate between genetic and environmental effects. The following analytical classification of subjects was therefore used (see Figure 1).

Assessment of personality

In order to assess personality traits we used the framework of the Big Five model of personality (Costa & McCrae, 1992; Goldberg, 1990; McCrae & Costa, 1999), which is particularly appropriate for evolutionary personality research (Buss, 1991; Penke, Denissen, & Miller, 2007b; Nettle & Penke, in press). We used an adjective-based questionnaire, developed in the Italian language and widely validated in various Italian samples; internal reliability and inter-correlation of the subscales are reported in Perugini (Caprara & Perugini, 1994) and Piconi (Piconi, 1998). This questionnaire consists of 50 adjectives taken from a pool of adjectives widely used for personality assessment in Italian subjects (Di Blas & Perugini, 2002), ten adjectives for each of the five personality dimensions, five with positive and five with negative polarity. For each adjective the subject had to rate how much it describes him on a 7-point scale. Individual scores were computed as a total of the response values for each factor, after inverting the scale for the negative items. Questionnaires were handed out by the assistants in person, self-administered by the subjects, and immediately recollected.

Statistical analysis

Standardized *T*-scores (with mean = 50 and standard deviation = 10) were used to compare personality traits between populations (Benjamin et al., 1996; Ebstein et al., 1996; Terracciano et al., 2005; Allik, Mõttus, Realo, Pullmann, Trifonova, & McCrae, 2009). The *T*-scores were computed by standardizing the raw scores with reference to the distribution of the Mainlanders control sample, thus allowing a comparison with the previous work (Camperio Ciani et al., 2007).

Many studies have reported significant correlations between personality traits and sex, age and educational level (Costa, Terracciano, & McCrae, 2001; Feingold, 1994; Goldberg, Sweeney, Merenda, & Hughes, 1998). This finding was confirmed in our sample by a preliminary stepwise

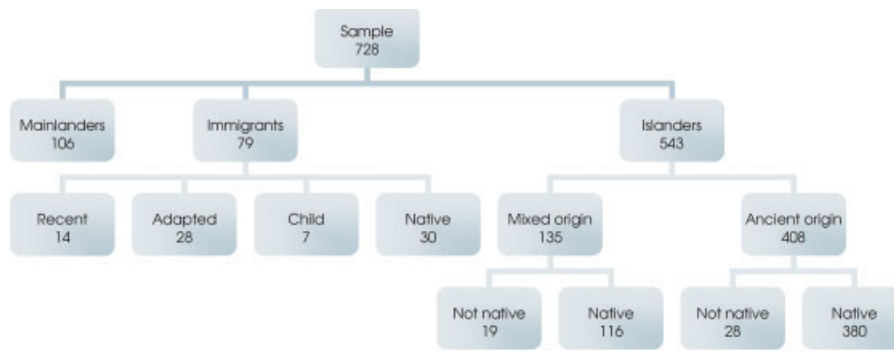


Figure 1. Sample classification. *Mainlanders*: subjects resident and born in the Trapani area, on mainland Sicily, with no known relatives coming from the Egadi archipelago. *Islanders*: subjects resident in the Egadi archipelago with at least one grandparent native to the islands; most of them were born in the islands (*Native*), but some of them were born incidentally on the mainland (*Not native*). *Ancient Origin Islanders*: a subset of Islanders subjects with all four grandparents native to the islands; according to the historical accounts most of them descend directly from the founders of the island population. *Mixed Origin Islanders*: a second subset of Islanders with 1–3 grandparents native to the islands. *Immigrants*: subjects resident in the Egadi archipelago without grandparents native to the islands; they include all 1st, 2nd and 3rd generation immigrants to the archipelago, with origins in various parts of Italy; they are further classified into four subsets. *Adapted Immigrants*: immigrants resident for at least 20 years, who immigrated after 10 years of age; these individuals have shared the island environment with islanders for a long time but do not have recent ancestry in common. *Recent Immigrants*: immigrants resident for less than 20 years who immigrated after 10 years of age; these individuals share the least environment and genetic ancestry with islanders. *Child Immigrants*: subjects who immigrated before 10 years of age; these individuals have shared the same environment with islanders since infancy; this group is dealt with separately because early experience could influence adult personality traits. *Native Immigrants*: 2nd and 3rd generation immigrants (i.e. descendants of immigrants) born on the Egadi islands; they have shared with islanders the same environment and early experience since birth but have no recent shared genetic ancestry. In order to investigate which mechanism could be at the origin of personality differences, we further classified the *Islanders* into *Emigrant* and *Sedentary*, according to whether they had emigrated from the island during their lifetime. *Emigrant*: subjects who emigrated permanently (not just for the purposes of studying), to mainland Italy or another country and started a family away from the island. Some of these individuals were sampled on the nearby mainland (Trapani), others were sampled in the islands during a family visit or as they returned to the island, once retired, at a late age. *Sedentary*: islanders who never left the island during their lifetimes, if not for the purposes of studying.

regression analysis (we found significant effects for sex and age on *conscientiousness* and *emotional stability*, and for all the three variables on the other traits). To eliminate the effect of sex, age and education level on group comparisons, all the statistical tests reported in the paper (p -values summarized in Tables 2 and 3) were obtained by ANCOVA with sex, age and education level as covariates¹. Comparisons between groups with less than 20 subjects were not considered. For each significant comparison, we reported the T -score difference estimated by the ANCOVA model to evaluate the effect size.

RESULTS

For each sub-sample we reported sex, age, education level, age at the time of immigration and years lived on the islands by immigrants in Table 1. We reported, for each subgroup considered in the analysis, the Big Five personality traits expressed in T -scores in Figure 2, to estimate the measured personality mean T -scores in each population subset.

First question. Are there differences in personality traits between islanders and mainlanders?

Islanders ($n = 528$) differ from mainlanders ($n = 106$) on *extraversion* and *openness to experience* after controlling for the effect of the covariates (Figure 3): islanders were significantly less *extraverted* and less *open to experience* (-8.3 and -6.0 corrected T -scores,² respectively). The other

¹The Kolmogorov–Smirnov and the Shapiro–Wilk normality tests showed that the normality assumption held up for personality traits scores distribution.

²Effect size estimate: T -scores difference estimated by the ANCOVA model with sex, age and education as covariates.

differences were not significant (Table 2). A further comparison between mainlanders and the subset of native islanders with ancient origin ancestry ($n = 380$) shows a highly significant difference for *extraversion* ($p < .001$), *openness to experience* ($p < .001$) (-9.8 and -6.6 corrected T -scores, respectively), and a significant difference for *conscientiousness* ($p = .042$). While for *emotional stability* the difference was on the critical level ($p = .051$) (Table 2).

Second question. Can these differences be ascribed to a possible genetic origin, or are they due to individual flexible adaptation to the environment?

In Table 2 we show that immigrants ($n = 79$) did not differ from mainlanders ($n = 106$) on any traits except *emotional stability* ($+2.9$ T -scores, $p = .035$). Immigrants significantly differed from original islanders ($n = 408$) on *extraversion* ($p < .001$) and *openness to experience* ($p = .001$) ($+7.3$ and $+4.1$ T -scores, respectively). The subjects who immigrated to the islands showed a personality profile that was undistinguishable from the mainland population, except for higher *emotional stability*; in contrast, immigrants were significantly more *extraverted* and more *open to experience* than islanders (Figure 4).

To better discriminate between genetic and environmental hypotheses, in Table 3 we show eight new comparisons of relevant sample subsets. The first part of Table 3 tests the effects predicted by the *genetic hypothesis*; the second part of the table tests differences predicted by the *individual flexible response to the environment hypothesis*.

The first and second ‘genetic’ comparisons aim to detect the effect of possible genotype differences between subsets of *immigrants* and *islanders* who have shared the same environment; the third comparison aims to detect a gradient

Table 1. Gender, age, education level, age at the time of immigration and years lived on the islands by immigrated people

Sample subsets		Gender	Age	Education	IMM. age	IMM. years
Mainlanders						
(N = 106)	Mean	0.41	40.25	10.16	—	—
	Std. error	0.05	1.57	0.40		
Immigrant						
ADAPTED (N = 28)	Mean	0.54	54.39	10.25	25.82	28.57
	Std. error	0.10	2.34	0.813	2.04	1.42
RECENT (N = 14)	Mean	0.57	44.50	8.21	33.14	11.36
	Std. error	0.14	3.65	0.78	3.64	1.72
CHILD (N = 7)	Mean	0.86	35.86	12.29	4.00	31.86
	Std. error	0.14	2.22	0.71	0.54	2.44
NATIVE (N = 30)	Mean	0.37	39.03	9.00	—	—
	Std. error	0.09	3.48	0.70		
MIXED ORIGIN ISLANDERS						
NOT NATIVE (N = 19)	Mean	0.58	44.32	9.58	24.84	19.47
	Std. error	0.12	3.71	1.13	4.11	2.81
NATIVE (N = 116)	Mean	0.52	42.61	8.98	—	—
	Std. error	0.05	1.70	0.34		
ANCIENT ORIGIN ISLANDERS						
NOT NATIVE (N = 28)	Mean	0.43	42.82	9.61	24.96	17.86
	Std. error	0.10	3.22	0.75	2.72	3.08
NATIVE (N = 380)	Mean	0.48	47.90	8.10	—	—
	Std. error	0.03	0.91	0.19		

Gender: 0 = male, 1 = female. For Gender, the reported mean is the fraction of females in the subset.

Education: years of study.

Mainlanders: subjects resident and born in Trapani town, in mainland Sicily with no known relatives coming from the Egadi archipelago. Islanders: subjects resident in the Egadi archipelago with at least one grandparent native to the islands; most of them are native to the islands, but some of them were born on the mainland. Ancient Origin Islanders: subjects resident in Egadi with all four grandparents native to the islands; according to the historical accounts most of them descend directly from the founders of the island population. Mixed Origin Islanders: subjects resident in Egadi with 1–3 grandparents native to the islands. Immigrants: subjects resident in the Egadi archipelago without grandparents native to the islands; they include all immigrants of the 1st, 2nd or 3rd generation to the archipelago, coming from all over Italy. Adapted Immigrants: immigrants resident for at least 20 years, who immigrated after 10 years of age; these individuals have shared the island environment with islanders for a long time but do not have recent ancestry in common. Recent Immigrants: immigrants resident for less than 20 years who immigrated after 10 years of age; these individuals share with islanders the least of both environmental and genetic ancestry. Child Immigrants: subjects who immigrated before 10 years of age; these individuals have shared the same environment with islanders since infancy; this group was dealt with separately because early experience could influence adult personality traits. Native Immigrants: 2nd and 3rd generation immigrants (i.e. descendants of immigrants) born on the Egadi islands; they have shared with islanders both the same environment and early experience since birth but have no recent shared genetic ancestry.

effect in the genotype expression by comparing *native mixed origin islanders* (1–3 grandparents native to the islands) with *native ancient origin islanders* (all four grandparents native to the islands). Indeed, when comparing *native immigrants* (n = 30) and *native ancient origin islanders* (n = 380), both of whom shared the insular environment since birth, we found that the former to be significantly higher in *extraversion* (+8.6 T-scores, $p < .001$) and *openness to*

experience (+4.1 T-scores, $p = .020$), and lower in *conscientiousness* (–4.5 T-scores, $p = .004$). Furthermore, comparing *adapted immigrants* (n = 28) and *non-native ancient origin islanders* (n = 28), both of whom were born and spent their infancy on the mainland before coming to live on the islands, we found the former significantly higher only in *extraversion* (+7.4 T-scores, $p = .026$); moreover, comparing *native mixed origin islanders* (n = 116) and

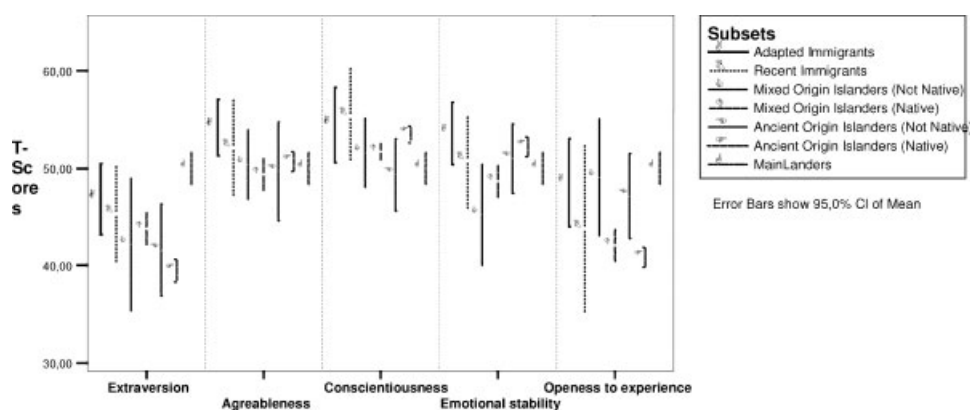


Figure 2. Big Five personality traits measured in the sample subsets, expressed in T-scores. T-scores are standardized scores with mean = 50 and standard deviation = 10, computed by standardizing the raw scores with reference to the mainland control sample.

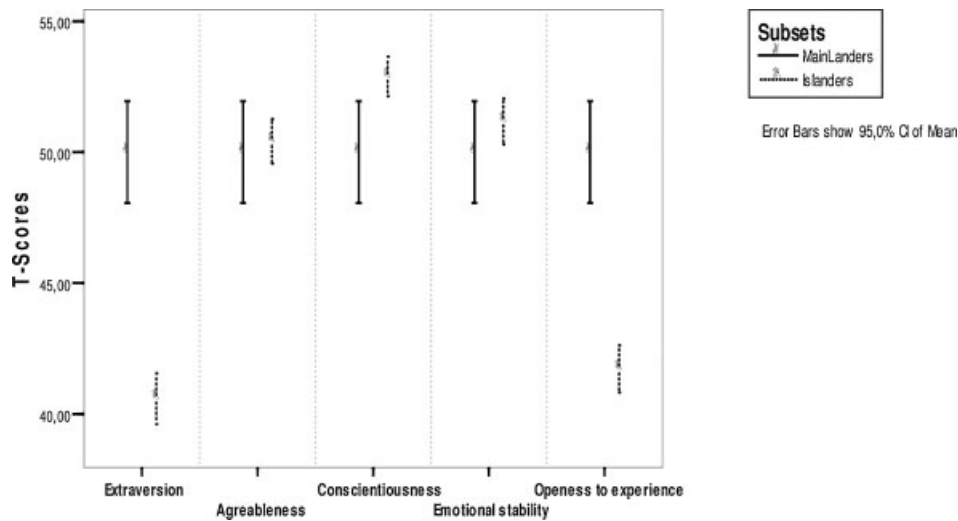


Figure 3. Islanders versus Mainlanders.

Table 2. Egadi personality traits assessment

	Subsets comparison	N	Extra version	Agreeable ness	Conscient iousness	Emotional stability	Openness to experience
1	ISLANDERS	543	-8.30	-0.01	+1.50	+1.17	-5.96
	MAINLANDERS	106	0.000	0.991	0.093	0.269	0.000
	NATIVE ANCIENT ORIGIN ISLANDERS	380	-9.83	+0.41	+1.93	+2.12	-6.58
	MAINLANDERS	106	0.000	0.717	0.042	0.051	0.000
	IMMIGRANTS	79	+7.28	+0.58	-1.14	+0.61	+4.10
	ANCIENT ORIGIN ISLANDERS	408	0.000	0.642	0.262	0.593	.001
2	IMMIGRANTS	79	-1.58	+0.87	+0.60	+2.90	-1.66
	MAINLANDERS	106	0.269	0.537	0.966	0.035	0.254
	ANCIENT ORIGIN ISLANDERS	408	-9.65	+0.33	+1.67	+2.04	-6.22
	MAINLANDERS	106	0.000	0.771	0.074	0.057	0.000
3	EMIGRANT ISLANDERS	167	+3.69	+0.20	-0.48	+0.73	+4.00
	SEDENTARY ISLANDERS	376	0.001	0.836	0.546	0.449	0.000
	EMIGRANT NATIVE ISLANDERS	153	+3.93	+0.13	+0.05	+0.90	+3.56
	SEDENTARY NATIVE ISLANDERS	343	0.001	0.899	0.953	0.367	0.000

For each comparison, the T-score difference estimated by the ANCOVA model with age, gender and education as covariates, is reported in order to evaluate the effect size, followed by the significance of the difference.

Bold value signify the comparisons between two different populations

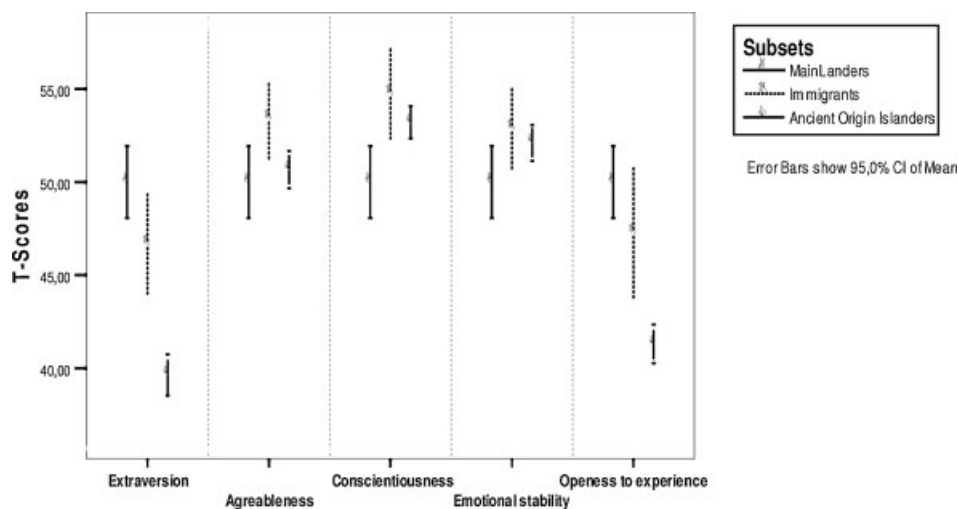


Figure 4. Mainlanders versus Immigrants versus Ancient Origin Islanders.

Table 3. Genetic and environmental hypotheses

Subsets comparison	N	Extra version	Agreeableness	Conscientiousness	Emotional stability	Openness to experience
GENETIC HYPOTHESIS						
NATIVE IMMIGRANTS	30	+ 8.60	-1.25	- 4.51	-0.22	+ 4.11
NATIVE ANCIENT ORIGIN ISLANDERS	380	0.000	0.513	0.004	0.903	0.020
ADAPTED IMMIGRANTS	28	+ 7.36	+1.70	+0.97	+3.09	+3.14
NOT NATIVE ANCIENT ORIGIN ISLANDERS	28	0.026	0.581	0.695	0.222	0.317
NATIVE MIXED ORIGIN ISLANDERS	116	+ 3.99	-1.27	-1.00	- 3.08	+0.22
NATIVE ANCIENT ORIGIN ISLANDERS	380	0.001	0.232	0.243	0.003	0.826
Environmental hypothesis						
ADAPTED IMMIGRANTS	28	-0.10	+2.31	+0.76	+ 4.90	+1.15
MAINLANDERS	106	0.965	0.290	0.727	0.025	0.604
NATIVE IMMIGRANTS	30	-2.02	-0.97	-2.54	+1.35	-2.81
MAINLANDERS	106	0.291	0.638	0.215	0.489	0.133
NATIVE IMMIGRANTS	30	-2.23	-1.82	-1.26	-2.57	-3.60
ADAPTED IMMIGRANTS	28	0.387	0.476	0.662	0.284	0.177
NATIVE ISLANDERS	496	-0.55	+0.46	+2.37	+2.56	- 5.32
NOT NATIVE ISLANDERS	47	0.754	0.762	0.054	0.088	0.000
NATIVE ANCIENT ORIGIN ISLANDERS	380	-1.50	+0.88	+ 3.17	+1.17	- 4.42
NOT NATIVE ANCIENT ORIGIN ISLANDERS	28	0.675	0.662	0.044	0.531	0.018

For each comparison, the *T*-score difference estimated by the ANCOVA model with age, gender and education as covariates is reported in order to evaluate the effect size, followed by the significance of the difference *p*-values.

Bold value signify the comparisons between two different populations

native ancient origin islanders ($n = 380$), both of them sharing the same island environment but different genetic ancestry, we found the former significantly more *extraverted* (+4.0 *T*-scores, $p = .001$) and less *emotionally stable* (-3.1 *T*-scores, $p = .003$).

In the second part of Table 3, the first 'environmental' comparison measures the effect of living for a long time in the insular environment on the adapted immigrants, the second one shows the effect on the native immigrants of living on the islands since birth, the additional three comparisons test the influence of the infancy environment on immigrant and islander personality, the so-called *Early Experience* hypothesis. In this case, comparing *adapted immigrants* and *mainlanders*, who belong to the same mainland population but did not share the same environment for a long time, we found that the former show no differences from *mainlanders* for all traits except for higher *emotional stability* (+4.9 *T*-scores, $p = .025$). Comparing *native immigrants* and *mainlanders*, who did not share the same environment since birth, we found that *native immigrants* do not differ from the mainland population on any personality traits. Comparing *native immigrants* and *adapted immigrants*, the former differ for having had their early experience on the island: we found that *native immigrants* show no differences from *adapted immigrants* on any personality traits. In a comparison of *native islanders* and *non-native islanders*, the former differs for having had early experience on the island: we found that *native islanders* are less *open to experience* (-5.3 *T*-scores, $p < .001$) and possibly more *conscientious* (+2.4 *T*-scores, $p = .054$) than *non-native islanders*. Finally, when comparing *native ancient origin islanders* and *non-native ancient origin islanders*, the former differs in that that have had early experience on the island: we found that *native ancient origin islanders* are less *open to experience* (-4.4 *T*-scores, $p = .018$) and more *conscientious* (+3.2 *T*-scores, $p = .044$) than *ancient origin islanders* born on the mainland.

Third question. Which mechanism could be at the origin of these differences?

In order to investigate if emigration was at the origin of such differences, we examined all *islanders* (native and non-native, $n = 543$) subdivided, in Table 2, into those who emigrated during their own lifetime from the island ($n = 167$) and those who never left the island ($n = 376$). Islanders who emigrated from the islands are significantly more *extraverted* ($p = .001$) and more *open to experience* ($p < .001$) than the *sedentary* (non-emigrated) insular population (+3.7 and +4.0 *T*-scores, respectively). In Figure 5 we show the corrected *T*-scores of emigrants versus *sedentary*, referred to average *T*-scores of mainlanders, which is always 50. It can be noted that *emigrants* are significantly more *extravert* and *Open to experience* than *sedentary* islander but, as all other islanders, they are significantly less *extravert* and *open to experience* than *mainlanders*. We then restricted the comparison to the subset of *native islanders* only ($n = 496$, Table 2), to exclude the possible confounding effect of individuals not born on the island, and we obtained the same results.

DISCUSSION

The results of our study shown in Table 2 parallel previous findings from the study of other Italian archipelagos (Camperio Ciani and Ceccarini, 2002; Camperio Ciani et al., 2007). Islanders are always significantly less *extraverted* and *open to experience* than mainlanders. We have shown that subjects who immigrated to the islands retain a personality profile, which is undistinguishable from the mainland population, except for higher *emotional stability*; in contrast, immigrants are more *extraverted* and more *open to experience* than islanders. These results are more

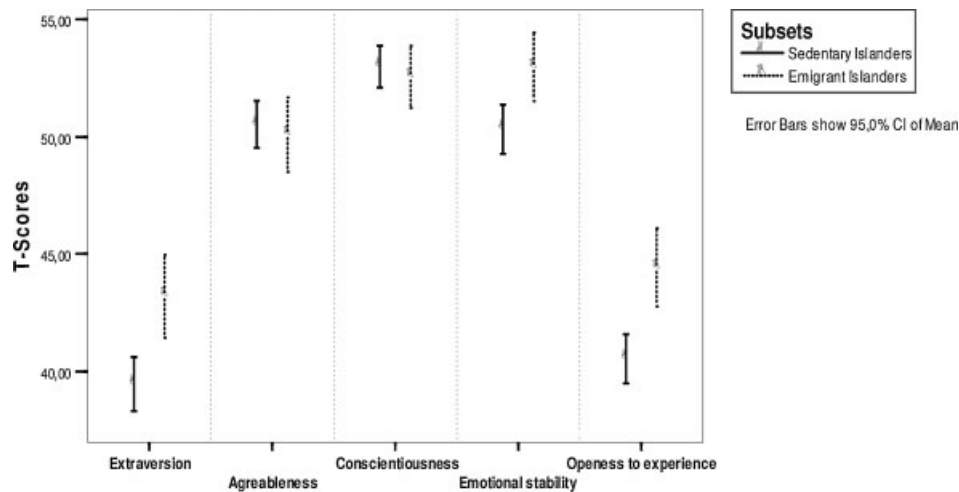


Figure 5. Emigrant Islanders versus Sedentary Islanders.

consistent with the genetic predictions than the environmental ones (Table 3). Indeed, immigrants did not change their personality profile after immigrating to the insular environment and remained different from islanders.

Founder effect hypothesis

We have additional evidence against the alternative hypothesis suggested by Van Oers (2007) that the personality of the founding populations of the islands previously studied was different from the mainlanders right from the beginning, as per the founder effect (Fisher, 1930). Already Camperio Ciani et al. (2007) observed the same pattern of personality differences in three different archipelagos, and in this study we again observed almost exactly the same pattern of differences in another one, with a rather different historical background. We here show in a comparative table (Table 4) between this study and the previous one that except minor difference in effect size *Extraversion*, and *Openness to experience* show always the same pattern of differences, conscientiousness has only a minor difference when comparing emigrants and sedentary islanders, and the other two traits never show any significant differences. Hence, at present, after about 25 generations, we have observed four independent archipelagos (including the ones considered in the previous study), composed of 15 inhabited islands in total, showing a convergent personality pattern (Table 4). It is

unlikely that this is the result of multiple and similar founder effects.

Genetic versus environmental hypotheses

The *adapted immigrants*, after living in the island environment for 20 years or more, still preserve most of their original mainlander personality (Table 3); also the *native immigrants*, despite having been born on the islands, differ neither from *mainlanders* nor from *adapted immigrants* on any personality trait; the *native immigrants*, in contrast, differ from the *native original islanders* (with whom they have shared the same environment since birth) on *extraversion*, *openness to experience* and *conscientiousness*. These results are not consistent with an environmental influence on these personality traits, and suggest genetic implications.

In particular, the *Early Experiences* hypothesis (Costa & McCrae, 1992; Forgas & Van Heck, 1992; McCrae & Costa, 1999) is not supported by the present findings as far as *extraversion* is concerned. The whole set of comparisons presented in Table 3 is consistently significant for all the comparisons which lend support to the genetic hypothesis, while *extraversion* does not confirm any of the environmental predictions. This suggests that *extraversion* is a fairly stable, endogenous trait, and is neither significantly influenced by the environment, nor by early experiences

Table 4. Comparison between the studies of Camperio Ciani et al. (2007), and present one

		Extraversion	Agreeableness	Conscientiousness	Emotional stability	Openness to experience
Islanders vs. mainlanders	Camperio Ciani et al. (2007)	–		+		–
	Present study	– –		+		– –
Islanders vs. immigrates	Camperio Ciani et al. (2007)	–				– –
	Present study	– –				– –
Emigrates vs. islanders	Camperio Ciani et al. (2007)	++		–		++
	Present study	++				++

Camperio Ciani et al. (2007) study includes three archipelagos with a total of ten inhabited islands and the present one includes one archipelago with three inhabited islands.

Traits higher, less (+) or more (++), than three standardized *T*-scores difference. Traits lower, less (–) or more (– –), than three standardized *T*-scores difference. Only significant differences are shown in the table.

during childhood, as is shown in the present study. Hence, this trait is rather likely to have an important genetic basis.

Our research design cannot exclude the possible role of parental education on *native immigrants*, however, many studies have found minimal evidence for the role of parental education on personality development (Dunn & Plomin, 1991; Krueger, 2000; Turkheimer, 2000).

One framework that tries to investigate human behaviour is the gene–environment interaction framework (O'Connor et al., 2003; Plomin & Crabbe, 2000; Plomin et al., 1994; Reiss et al., 2000). Penke highlighted the role of gene–environment interactions in the study of personality (Penke et al., 2007), that is the interactions between genetic factors and individual flexible responses to the environment, or phenotypic plasticity (West-Eberhard, 2003). For *openness to experience*, the gene–environment interaction seems to be the paradigm that better explains our results. Indeed, the difference between native immigrants and native original islanders suggests a genetic influence does exist, because these two groups of subjects have shared the same environment since birth, while they are likely to come from relatively different gene pools. On the other hand, an influence of early experience and environment on this trait matches with the differences found in the comparisons between *native* and *non-native islanders*; however, the fact that *native immigrants* do not differ from *adapted immigrants* and *mainlanders*, does not support this conclusion. Similarly, conflicting results are found for *conscientiousness*. Thus, we suggest that for these two traits a genetic influence exists, but it might be interacting with the effects of early experience and the individual flexible response to the environment.

Personality Gene Flow hypothesis

We propose the *Personality Gene Flow* hypothesis to explain personality differences found in small isolated populations. The *Personality Gene Flow* hypothesis suggests that it is the combined effect of a reduced and random immigration flow associated with a strong and non-random emigration flow that can rapidly produce personality differences in a small population.

Our study suggested that Egadi emigrant islanders scored higher on *extraversion* and *openness to experience* in comparison to sedentary people who never left the islands. More extravert and open to experience individuals seem to have a higher propensity to emigrate: this interpretation is supported by the results of molecular genetic studies, affirming a correlation between *extraversion* and *novelty-seeking* (Benjamin et al., 1996) and by results of population studies showing that novelty seekers tend to emigrate more (Chen, Burton, Greenberger, & Dmitrieva, 1999). If these traits were influenced by specific alleles, then it could be that they were progressively removed from the island population gene pool.

A possible criticism is that emigrants could have changed their traits after emigrating, rather than their traits having a causal role in their emigration. However, we have confirmed above that *extraversion* is a very stable endogenous

personality trait, and furthermore it seems that *openness to experience* is also unlikely to change in adulthood. Given that mainlanders who immigrated to the islands conserved their original personality, we deduce that island emigrants should also retain their traits in the new environment.

Rebollo and Broomsma (Rebollo & Boomsma, 2007) suggested *Inbreeding Depression* as an alternative explanation for low *extraversion* and *openness to experience* in islanders, but as Penke (Penke et al., 2007) noted, it is especially striking that inbreeding depression should exclusively affect traits that can be directly associated with migration tendencies and active niche selection (i.e. *openness to experience* and *extraversion*). The worldwide distribution of DRD4 polymorphisms suggests that carriers of the allele, which has been associated with high sensation seeking, are more likely to migrate (Chen et al., 1999). In our study, the most extravert *native islanders* are found within those who emigrated. The *Inbreeding Depression* hypothesis, contrary to the *Personality Gene Flow* hypothesis, does not predict different allele frequencies within a small population. A direct genetic study of allele frequencies in the island population will clarify this question.

Penke and colleagues assess three evolutionary genetic mechanisms that could explain genetic variance in personality within large populations (selective neutrality, mutation–selection balance and balancing selection). Based on evolutionary genetic theory and empirical results from behaviour genetics and personality psychology, they suggest that mutation–selection balance seems best able to explain genetic variance in intelligence, while balancing selection by environmental heterogeneity seems best able to explain genetic variance in personality traits (Penke et al., 2007). Camperio Ciani et al. suggested that the alleles influencing personality might also vary their frequency between populations due to emigration and consequent gene flow as an additional genetic mechanism in small populations (Camperio Ciani et al., 2007). This hypothesis would be consistent with the interactionist perspective (Barrick & Mount, 1991; Hettema & Kenrick, 1992; Tett, Jackson, & Rothstein, 1991) that proposes that people with particular personalities actively look for the best fitting environment and are ready to displace themselves to find it, hence removing their alleles from the original population. In a prospective study on Finnish people and another study on US citizens who migrated within or between states, Jokela found that *extraversion* and *openness to experience* are both strong predictors of migration propensity (Jokela, 2009; Jokela, Elovainio, Kivimäki, & Keltikangas-Järvinen, 2008). We suggest that extraverted and open to experience subjects tend to leave the confined environment of the island because it offers few perspectives and opportunities, thus decreasing the frequency of alleles influencing extraversion. At present, however, we can only speculate as to what induces open to experience and extravert people to leave the islands and future longitudinal prospective studies are needed in order to answer this point.

Fisher's classic work on the effect of gene flow on a small population shows that it is not necessary for immigration to be completely absent in order to progressively produce

differences in the phenotype. Whenever the outflow of particular alleles, due to emigration, is not replaced by a corresponding inflow of the same alleles in the population, we can expect a progressive reduction in the frequency of that allele, generation after generation (Fisher, 1930). After a sufficient number of generations this frequency reduction should be measurable in the phenotype expressed by those alleles. The difference between outflow and inflow rates and the number of generations that the gene flow process has been active constitute critical factors.

Immigration to small islands, and other small confined environments, in the past has been random personality-wise, because it was determined by exogenous life events, which were unrelated to personality. In our study's case, immigrants to the Egadi islands were not selected on the basis of personality traits (Calleri, 2006). Only very recently has tourism attracted a few individuals to a permanent and voluntary settlement in the archipelago. We suggest that this condition holds true for a majority of isolated populations. In the past, before the advent of modern tourism, very few people deliberately decided to resettle in a small remote isolated community.

As an alternative to the *Personality Gene Flow* hypothesis, Chen et al. (1999) suggest that selective mortality on individuals who emigrate to new environments favors extravert and open to experience individuals, while in their native environment, it favors introverted and closed individuals, who are more attached to the land (Chen et al., 1999). However, in these Italian archipelagoes the change in frequency of the personality traits happened quickly, in relatively few generations and with no particular mortality recorded (Gallitto, 2008; ISTAT, 2009). Hence, selective mortality is unlikely to be the mechanism responsible for the differences in personality traits observed.

Various explanations have been suggested to explain why many alleles influencing personality are not selected against and removed from large populations (Buss, 1991, 1999; Dawkins, 1977; Mealey, 1995; Tooby & Cosmides, 1990). We here suggest that the active human-environment interaction explains why no measurable differences of personality are found in wide-scale population surveys (such as national ones). In large populations gene flow happens within the same population, as people displace from one environmental niche to the other within the same city, area or country, hence large-scale personality investigations cannot detect any group differences. On the contrary, significant measurable differences can be found in a small isolated environment, as is the case with the Egadi archipelago studied here. In small isolated populations, where the socio-environmental niches are limited and cannot fit each possible personality profile, people that do not adapt, do not die but they do migrate elsewhere. In this case, gene flow happens between populations, then personality studies can detect population personality differences between populations because emigrants (and their descendents), after having abandoned the island, are no longer present there and remove their alleles from the isolated population.

In conclusion, we propose here that if the *Personality Gene Flow* hypothesis holds true, then personality differ-

ences in small relatively isolated populations should rapidly appear over time wherever there is strong non-random emigration paired with random and reduced immigration, as is the case in most isolated small populations in the world, such as small islands or isolated high mountains communities. Further research is necessary to increase the external validity of our hypothesis, perhaps in very different geographic locations with different historical backgrounds. Our results are based on questionnaires and genetic factors are estimated by demographic variables (ancestry, pedigree), not by direct genetic tests, and we can only indirectly point to possible underlying microevolutionary changes. A further study based on genetic tests is needed to support our arguments that assume the association between ancestry and alleles. Our hypothesis predicts that future genetic investigations will find significantly different allelic frequency distributions between isolated small populations and corresponding large ones, but only for genes, which influence traits of *Extraversion* and *Openness to experience*. This study further underlines the adaptable nature of our species, which responds to environmental challenges not only by selecting physical traits but also by selecting behavioural and personality traits.

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