Original study

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Peninsular effect on species richness in Italian small mammals and bats

Abstract: Peninsular effect is an anomalous gradient in plant and animal species richness from base to tip of a given peninsula. This pattern has been studied intensely on various taxonomic groups, but with scarce attention for using standardized data. Here, using presence-absence data normalized by the field effort, the peninsular effect on the species richness of some mammalian groups (Eulipotyphla [i.e. Soricomorpha + Erinaceomorpha], Rodentia, and Chiroptera) was analyzed along the Italian peninsula. Specifically, species richness at each 30′-wide latitudinal band and the normalized species richness were compared, and generalized linear models (GLM) were used to assess whether habitat diversity, altitudinal range and area of each latitudinal band were the main predictors in explaining the peninsular effects in each of the three mammalian orders. In both Rodentia and Chiroptera, species richness was better predicted by habitat heterogeneity and by the interaction term habitat heterogeneity × field effort. For Eulipotyphla, GLM models gave no significant results. Our study highlighted the importance of taking into account the sampling effort in order to proper evaluate the peninsular effects on species richness in animals.

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1 Introduction

A progressive reduction in plant and animal species richness from base to tip of North American peninsulas has been observed since several decades ('peninsula effect'; Simpson 1964). This biogeographic gradient is a complex phenomenon including species-specific processes and equilibrium dynamics where no single predictor acts alone (Means and Simberloff 1987; Murphy 1990; Raivio 1988; Seib 1980; Taylor and Regal 1978; Wiggins 1999). Pattern in species richness is more evident when comparing species richness to equally sized mainland regions (Simpson 1964). The main Simpson's hypothesis was that the observed patterns could be explained in terms of extinction/immigration dynamics related to the theory of insular biogeography (TIB). That is, peninsular geometry may act to hinder immigration and increase extinction (MacArthur and Wilson 1967; Simpson 1964). Following this hypothesis, peninsulas were considered 'semi-insulae' where immigration of individuals can proceed only from one direction (i.e. from their base; see reviews in Wiggins 1999; Battisti 2014). Moreover, local habitat factors could affect the various taxa (Busack and Hedges 1984; Due and Polis 1986; Lawlor 1983; Means and Simberloff 1987; Taylor and Pfannmuller 1981). Henceforth, to explain the "peninsular effect", a large number of different causal and context-dependent factors have been suggested, mainly referred to (1) recent stochastic processes and immigration–extinction dynamics (equilibrium and derived island biogeography theories: Simpsonian peninsular effect hypothesis, SPH; Simpson 1964), (2) area effect (per se and as a gradient), (3) historical processes (palaeoclimate and palaeogeography), (4) present circumstances (ecology, climate, geography), (5) natural and/or human-induced environmental heterogeneity and disturbances, (6) methodological artifacts (review in Battisti 2014).

Peninsula effects have been studied mainly on mammals, birds and butterflies (e.g., Kocher and Williams 2000; Taylor and Regal 1978). An apparent peninsular effect was observed, for instance, in heteromyids rodents and in bats in Baja California (Baquero and Tellería 2001; Lawlor 1983; Taylor and Regal 1978), in terrestrial mammals along the Korean oeninsula (Jo et al. (2017), and the Indochinese–Sundaic peninsula-island system (Woodruff and Turner 2009) and in small mammals along local peninsulas of Madagascar (Andrianjakarivelo et al. 2005).

Different responses to peninsular patterns may depend on the dispersal and vagility of the various taxa; for example, the patterns relative to bats were different from those relative to non-volant species (Taylor 1987). However, many peninsular patterns in species richness could be affected by the type of methods and analyses used (Battisti and Contoli 1997; Raivio 1988). The peninsula effect has often been assessed by counting presence-absence dots in regional atlases/databanks without sample sizes behind the presence-absence patterns, despite lack of species richness normalization in respect with the research effort may negatively affect the analyses (Battisti and Contoli 1997; Raivio 1988).

In this paper, using presence-absence data normalized by field effort, we analyze the peninsula effect on some mammalian groups (Eulipotyphla, i.e. Soricomorpha + Erinaceomorpha, Rodentia, and Chiroptera) along the Italian peninsula. Here, we compare:

 (i) The species richness at each latitudinal band with the normalized species richness;
(ii) Using generalized linear models (GLM), habitat diversity, altitudinal range and area of each latitudinal band species richness to select the main predictor variable in explaining the peninsula patterns in each of the three mammalian groups.

Since northern areas of the Italian peninsula (i) show a higher altitudinal range (from marine coasts to the Alps) and, consequently, a higher habitat diversity, and (ii) northern areas have been intensively studied when compared to southern areas, we hypothesize that, at least for the groups of studied mammals, (i)a north-south gradient of species richness is present and (ii) it could be affected by altitudinal range, habitat diversity, and sampling effort.

2 Materials and methods

2.1 Database

The territory of the continental (northern) and peninsular (central-southern) Italy (approximately lying within 12° of latitude) was subdivided from North to South into 24 latitudinal bands (LB, numbered from 1 to 24 north to south), each one comprising 30′ of latitudinal range and formed by a set of 1:100,000 IGMI (Italian Military Geographic Institute) map sheets of the same latitude. Since the LBs had not same area (generally larger in the northern LBs due to the shape of the Italian territory), we calculated using a GIS the total area (in m^2), as well as the minimum and maximum elevation (in m a.s.l.) in each LB (Appendix).

As source of presence data for the various species, we used CKmap 5.3.8 (English edition – version 5.4 – available for download at http://www.faunaitalia.it/documents/CKmap_54.zip) database. We considered only native species, excluding all allochtonous species. This database reports the taxonomical data and the distribution in Italy of Chiroptera, Rodentia, Eulipotyphla species. Species distribution was mapped attributing each record (i.e. the presence of a species in a single location) to the 10 × 10 km UTM cell (ED50 datum, MGRS system) on the basis of a gazetteer. The gazetteer stored in the database (available for download at http://www.faunaitalia.it/documents/TCI.zip) included 46,961 toponyms taken from the "Touring Club Italiano" (TCI) Atlas, accurately georeferenced using topographic maps of Italy at the scale 1:25,000. We deleted from the database all the records (i) reporting an inaccurate taxonomical classification (e.g. using open nomenclature instead of the Linnean binomials), and (ii) without collection date. Concerning the database, as we used data grouped by LB, it cannot be excluded that a few potential for pseudoreplication biases intrinsic to our dataset may be present (Ruggiero and Werenkraut 2007).

In the following text, we define the following variables: LB = latitudinal bands (growing from south towards north); see above; LBarea = area (m^2) of each LB; LBminel = minimum elevation (m a.s.l.) of each LB; LB maxel = maximum elevation (m a.s.l.) of each LB; LBrangealt = altitudinal range of each LB, that is: LBrangealt = LBmaxel – LBminel; HAB = number of habitats per LB, calculated as the total number of Corine Land Cover habitat types (level III) present inside each LB; S = number of species per LB; Dm = normalized species richness per LB as: Dm = S – $1/\ln N$ (Magurran 2004); N = research effort (i.e. total number of independent CKMap records in each LB).

2.2 Statistical analyses

In all analyses, given the small number of species, Erinaceomorpha are combined with Eulipotyphla. From the original database, for each LB we calculated HAB, N, S, and Dm. We correlated S and Dm against LB and HAB by using two-tailed Spearman rank correlation test (Dytham 2011). GLM were used to model LAT, HAB, and N and their interaction terms, and to assess their relationships with S (Hosmer and Lemeshow 2000). In the GLM model, S was used as the dependent variable and N as a covariate, and the identity link function and a normal distribution of error were used (McCullagh and Nelder 1989). We used the SPSS software for Windows (SPSS Inc. 2003). Alpha level was set at 0.05.

3 Results

From the CKMap data bank, we obtained 14,936 records (3902 for Eulipotyphla [i.e. Soricomorpha + Erinaceomorpha], 7143 from Rodentia, 3891 from Chiroptera). The
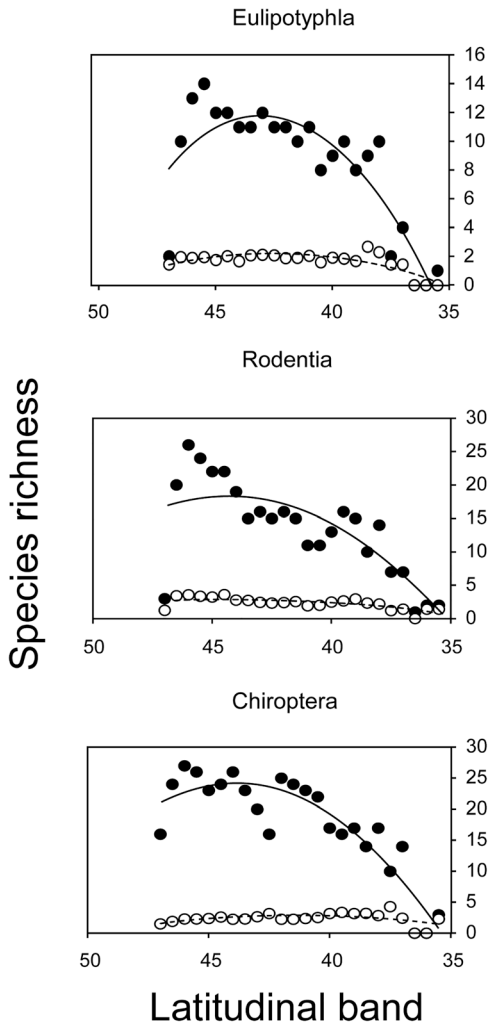
relationships between species richness and LB for the various mammalian groups are given in Figure 1, and those between species richness and HAB for the various mammalian groups are given in Figure 2.

Overall, LB and HAB were linearly correlated, with HAB increasing towards North ($r = 0.576$, $p = 0.003$, $n = 24$). HAB was also positively correlated with LBrangealt ($r = 0.482$, $p < 0.0001$); however, HAB was not affected by LBarea *per se* ($r = -0.320$, $p = 0.127$).

The synopsis of the general correlations among the various variables examined in the present study is given in Table 1. In all the examined mammalian groups there were significantly positive correlations (i) of S with both HAB and LB, and (ii) of Dm with both HAB and LB (Table 2). S was significantly correlated with LBarea in all the three studied orders (Eulipotyphla: $r = -0.501$, $p < 0.05$; Rodentia: $r = -0.463$, $p < 0.05$; Chiroptera: $r = -0.409$, $p < 0.05$), and it was also positively correlated with LBrangealt (Eulipotyphla: $r = 0.65$, $p < 0.0001$; Rodentia: $r = 0.789$, $p < 0.0001$; Chiroptera: $r = 0.737$, $p < 0.0001$; Figure 3).

Concerning the GLM, for Eulipotyphla, the low number of species and the low research effort produced a non-significant model ($F = 39.375$, $df = 22$, $p = 0.125$). For Rodentia, the general model was statistically significant ($F = 11.255$, $df = 18$, $p = 0.007$). In this model, S was predicted by HAB ($F = 8.547$, $p < 0.05$), and HAB $\times N$ ($F = 6.331$, $p = 0.012$), whereas N ($F = 3.778$, $p = 0.061$), LAT ($F = 3.346$, $p = 0.093$), and LAT $\times N$ ($F = 2.662$, $p = 0.123$) were not statistically significant. For Chiroptera, the general model was statistically significant ($F = 46.292$, $df = 18$, $p = 0.000$).

Figure 1: Relationships between species richness and 30′-wide latitudinal bands for the various mammalian groups. Filled dots indicate non-normalized data, and empty dots indicate normalized data. North–South direction: 24 (extreme North) − 1 (extreme South).
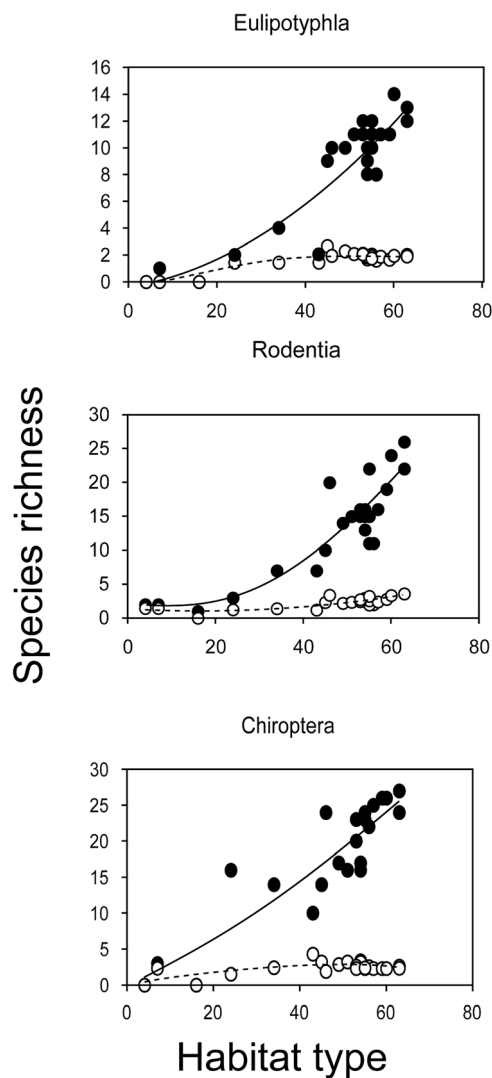
Figure 2: Relationships between species richness and habitat types for the various mammalian groups. Filled dots indicate non-normalized data, and empty dots indicate normalized data.

Table 1: Latitudinal band (LB), number of habitats per LB (HAB) versus number of species per latitudinal band (*S*), research effort in each latitudinal band (*N*), and normalized species richness per latitudinal band (Dm) for Eulipotyphla, Rodentia and Chiroptera.

LB	Hab	Eulipotyphla			Rodentia			Chiroptera		
		S	*N*	Dm	*S*	*N*	Dm	*S*	*N*	Dm
35.5	7	1	1	0	2	2	1.44	3	3	2.33
36	4	0	0	0	2	2	1.44	0	0	0.00
36.5	16	0	0	0	1	1	0	0	0	0.00
37	34	4	8	1.44	7	69	1.42	14	30	2.43
37.5	43	2	2	1.44	7	141	1.21	10	16	4.30
38	49	10	51	2.29	14	380	2.19	17	81	2.88
38.5	45	9	20	2.67	10	48	2.32	14	45	3.21
39	54	8	65	1.68	15	116	2.95	17	73	3.18
39.5	54	10	132	1.84	16	271	2.68	16	95	3.38
40	54	9	65	1.92	13	129	2.47	17	66	3.18
40.5	56	8	82	1.59	11	148	2.00	22	229	2.55
41	55	11	136	2.04	11	167	1.95	23	163	2.39
41.5	55	10	113	1.9	15	242	2.55	24	148	2.29
42	57	11	202	1.88	16	499	2.41	25	204	2.28
42.5	51	11	123	2.08	15	385	2.35	16	78	3.19
43	53	12	179	2.12	16	446	2.46	20	106	2.65
43.5	53	11	124	2.07	15	171	2.72	23	140	2.30
44	59	11	408	1.66	19	673	2.76	26	628	2.27
44.5	63	12	229	2.02	22	339	3.60	24	484	2.63
45	55	12	536	1.75	22	658	3.24	23	247	2.39
45.5	60	14	780	1.95	24	926	3.37	26	367	2.31
46	63	13	546	1.9	26	1062	3.59	27	397	2.33
46.5	46	10	98	1.96	20	263	3.41	24	246	1.92
47	24	2	2	1.44	3	5	1.24	16	45	1.50

Each latitudinal band covers 30′ in latitude. North-South direction: 24 (extreme North) − 1 (extreme South).

Table 2: Synopsis of the general correlations among the various variables examined in the present study.

	HAB	LB	LBarea	LBrangealt
Eulipotyphla				
S	<0.05	<0.05	<0.05	<0.05
Dm	<0.05	NS	NS	<0.05
N	NS	NS	NS	<0.05
Rodentia				
S	<0.05	<0.05	<0.05	<0.05
Dm	<0.05	<0.05	NS	<0.05
N	NS	NS	NS	<0.05
Chiroptera				
S	<0.05	<0.05	<0.05	<0.05
Dm	<0.05	<0.05	NS	NS
N	NS	NS	NS	<0.05

Symbols for the independent variables: latitudinal band = LB; number of habitats per latitudinal band = HAB; area (m^2) for each latitudinal band = LBarea; altitudinal range (m) for each latitudinal band = Lbrangealt. Symbols for the dependent variables: number of species per latitudinal band = *S*, normalized species richness per latitudinal band = Dm, and research effort in each latitudinal band = *N*. Each LB covers 30′ in latitude.

In this model, *S* was predicted by HAB ($F = 22.933$, $p < 0.001$), and HAB × N ($F = 11.789$, $p = 0.014$), whereas *N* ($F = 0.999$, $p = 0.363$), LAT ($F = 1.334$, $p = 0.106$), and LAT × N ($F = 1.213$, $p = 0.324$) were not statistically significant.

4 Discussion

Our data suggest that, at least in Rodentia and Chiroptera, the decrease in species richness towards South along the Italian peninsula were influenced mainly by HAB and, secondarily, by N and LBarea. Habitat diversity may affect peninsular patterns of species richness in different ways for the various taxa examined, as this variable can be interpreted as a proxy of primary productivity and structural complexity of the ecosystems (Krebs 1994; MacArthur 1964). Therefore, our data corroborate as the hypothesis that many peninsular patterns of different taxa merely reflect recent (i.e. post-Pleistocene) base-tip changes in
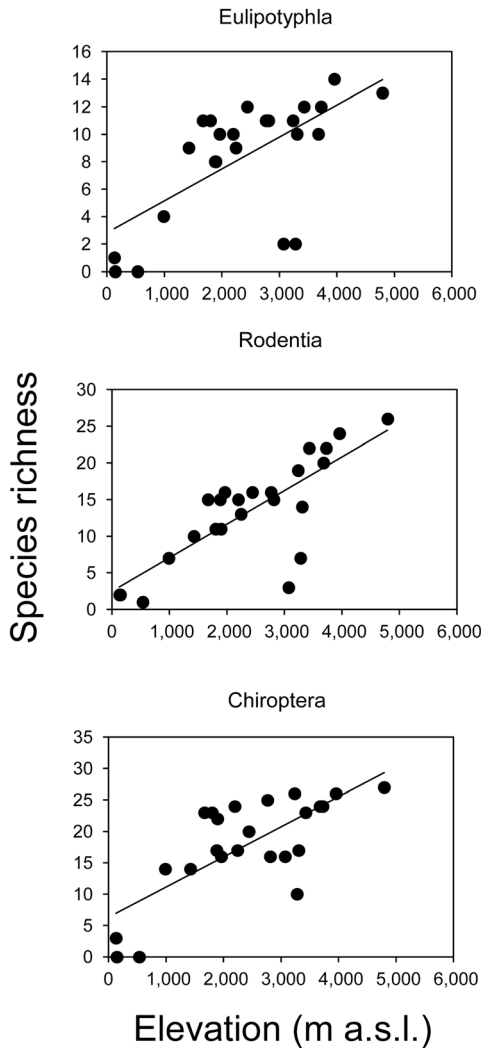
Figure 3: Correlation between altitudinal range in each latitudinal band and number of species per Latitudinal band for the three studied orders. For the statistical details, see text.

habitat diversity (Busack and Hedges 1984; Raivio 1988). In this regard, when controlling for habitat diversity effects, Johnson and Ward (2002) did not find a decrease in ant (Hymenoptera Formicidae) species richness towards the tip of Baja California. Also, Milne and Forman (1986) highlighted that differences in woody plant species richness were mainly due to environmental (bioclimatic) differences along a base-tip gradient in three North American small peninsulas.

We suggest that the environmental heterogeneity hypothesis (Milne and Forman 1986) may explain the deviation from the classic peninsular model, due to direct correlation between habitat diversity and species richness (see Tews et al. 2004), corroborating other evidences obtained by analogous biogeographical studies (e.g. Fløjgaard et al. 2011). For example, considering mammals in Mediterranean peninsulas, Barbosa and Benzal (1996) observed as in Iberian Peninsula the species richness pattern is indirectly driven by habitat heterogeneity, since it is most likely the result of the harsh conditions of the Mediterranean environments. Kryštufek (2004) observed different latitudinal patterns along the Balkan peninsula with clear hot spots in different groups, with non-volant mammals accumulating species more rapidly with increasing latitude than bats. In this peninsula the latitudinal pattern might be due to a species – area effect, with larger areas in Northern Balkans supporting more species when compared to Southern areas. Pooling data for different groups, a sharp decrease in species density occurred in different mammal groups at sub-peninsula level (Peloponnese Peninsula). However, at least in insectivores and rodents having lesser dispersal abilities when compared to bats, species patterns could be largely affected also by changes in habitat heterogeneity following a human-induced historical impact (clearance, burning and grazing, with consequent vegetational changes, ecosystem degradation and reduced resource availability; see also Kryštufek and Griffiths 1999).

In agreement with our study, it has been previously demonstrated that altitudinal range in latitudinal bands may affect habitat diversity (Tews et al. 2004; see also Andrianjakarivelo et al. 2005) because it provides different ecological (climatic, edaphic and vegetational) conditions, improving habitat availability for several species (Kocher and Williams 2000; for butterflies in South Korea see Choi 2004; for herpetofauna in Florida: Means and Simberloff 1987). Since altitudinal range may also affect resource availability at landscape/regional scale (Tews et al. 2004; see also Andrianjakarivelo et al. 2005), we suggest that the higher species richness in the LBs with higher altitudinal range may be explained with a higher local resource availability. Indeed, altitudinal range is correlated with habitat diversity.

Apart from the above-mentioned role of habitat diversity, we also observed that the research effort (N) is a further predictor explaining the peninsular patterns in species richness of both Rodentia and Chiroptera. While there is a considerable body of research available on these mammal groups from Northern Italy (the base of Italian

peninsula), the research effort has been comparatively less intense in Southern Italy (Gippoliti and Aloise 2016). A difference in sampling size from the base to the tip of the peninsula might explain the North–South gradient of number of species in Italy. Indeed, McCain (2003) highlighted that many analyses of peninsular patterns were obtained from not-standardized sampling design and protocols, thus affecting the debate on the driving forces explaining the peninsular patterns. For example, the number of species could be biased in areas where data are lacking, that generally correspond with the distal areas of peninsulas that are often more difficult to study. Consequently, these distal areas may appear impoverished in terms of species richness. In this regard, Jenkins and Rinne (2008) suggested that the study design, protocols and data analyses, controlling for sampling effort, should be clarified to avoid artifacts.

However, other factors could affect the observed patterns: climate, colonization patterns, historical and evolutionary, intrinsic patterns in species-specific abundance and anthropogenic factors. For example, at continental level, latitudinal pattern in species richness in European mammals can be interpreted on the basis of two different patterns of species-specific abundance distribution in which Palearctic species reduce their abundance from central-Europe outwards, while endemic, rare species show a similar depletion in the North (Baquero and Tellerìa 2001). At regional level, Cagnin et al. (1998) observed as differences among terrestrial small mammal coenoses in the tips of the Iberian and Italian peninsulas (Calabrian and Andalusian sites), could be climate-induced.

These factors, however, are not analyzed in the present study. The procedure of normalization could guarantee at least a comparison between number of species and research effort, as carried out in the present study. Indeed, our study uncovered that the peninsula patterns were less evident after normalization, as also the area effect that totally disappeared after normalization.

Taxonomic problems and uncertainty in diagnosis at species level may also contribute to generating anomalous patterns in diversity (Murphy 1990; Seib 1980). In recent decades, a growing body of evidence led to re-evaluate the taxonomic status of several southern Italian endemic taxa, some of them having been raised up to the full species rank

(e.g. Salicini et al. 2012; Wauters et al. 2017; for a review see Gippoliti and Groves 2018). It is therefore still unclear how the description of new cryptic species may affect the analyses on the peninsular effects as described in the present paper.

Overall, the decreasing diversity patterns of both Rodentia and Chiroptera along the North-South gradient can be also due to the kind of resources that they do find in the North and that are absent in the South: habitat heterogeneity is certainly the case (see also August 1983; Benton et al. 2003), and possibly also food resources may be correlated with habitat heterogeneity (Minshall and Robinson 1998; Rosenzweig and Abramsky 1980). Greater complexity allows them to obtain more food resources (Cromsigt et al. 2009) with indirect effects on predators abundance (McIntosh et al. 2004). And also, may lower predator–prey encounter rate (Atwood et al. 2009; Gorini et al. 2012).

Moreover, it should be remarked that, for a few species, the patterns may also have arisen from low sampling effort, thus introducing some potential biases in the analyses. For instance, Eulipotyphla exhibited the same peninsular effect patterns as Rodentia and Chiroptera, but at a non-statistically significant level. The absence of statistical significance in Eulipotyphla is almost certainly due to low sampling efforts accomplished with low taxonomic diversity. This low amount of data could hide the distribution pattern (peninsular effect) observed for Rodentia and Chiroptera.

In conclusion, our study highlighted the importance of taking into account habitat heterogeneity and the sampling effort in order to proper evaluate the peninsular effects on species richness. In this regard, future research could re-analyze data to corroborate or not the rôle of these variables to predict patterns of richness along peninsular gradients.

Appendix

Total area for each latitudinal band (LB, in m^2), as well as the minimum and maximum elevation (in m a.s.l.) in each 30′-wide LB of the Italian peninsula, and the altitudinal range in each LB (LBrangealt).

LB	Area	elev.min	elev.max	LBrangealt
35.5	199405198350021	−2	128	130
36	528444670091446	1	145	144
36.5	214544566783528	−7	526	533
37	507359194174105	−2	985	987
37.5	10631130966973	−2	3277	3279
38	113514169410599	−3	3306	3309
38.5	325773614608345	−4	1419	1423
39	634752955317833	−9	1873	1882
39.5	103434547338675	−6	1953	1959
40	128475206522096	−5	2238	2243
40.5	214105490424334	−9	1884	1893
41	185180701483454	−8	1792	1800
41.5	160958073570735	−7	2191	2198
42	150360800571877	−6	2762	2768
42.5	137509959904909	−8	2807	2815
43	14965936191886	−4	2438	2442
43.5	143399148029511	−7	1661	1668
44	149608885959833	−6	3229	3235
44.5	234175547459388	−9	3718	3727
45	242887892055649	−24	3404	3428
45.5	258746294370292	−20	3938	3958
46	226752553033012	−22	4771	4793
46.5	138673403956779	171	3851	3680
47	277206270811594	520	3590	3070

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