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'Peninsula effect' and Italian peninsula: materials for a review and implications in applied biogeography

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SUMMARY

'Peninsula effect' (a reduction of species number from base to tip along the peninsulas, more evident when comparing this parameter versus equally-sized mainland regions) appeared to be not a general pattern, but an occasional phenomenon shown in some species assemblages (communities, taxocenosis, ecological guilds) in specific contexts. These patterns can be different if related to different taxa, scales, ecological/taxonomic levels and no single theory was widely accepted to explain their causal processes. In this paper, an overview on a wide literature evidences as the causal factors/processes that might explain peninsular diversity patterns should be reconducted to following groups: 1) recent stochastic factors/processes (equilibrium and derived island biogeography theories); 2) historical events as paleoclimate oscillations, paleogeographic and tectonic changes ('diversity disequilibrium models'); 3) recent (deterministic) factors/processes (ecology, climate, geography), with a base-tip gradient; 4) anthropical recent factors/processes (habitat fragmentation and disturbances), with a base-tip gradient. A cautionary approach is requested when comparing, along a peninsular gradient, data from cells or bands at regional/landscape scale (γ -diversity level) or from single ecosystems/fragments (α -diversity level) because causal factors could be different in explain the observed patterns (respectively, heterogeneity at landscape scale and equilibrium dynamics).

Causal processes for 'inland/peninsulas' are different in respect to 'oceanic/geographic' ones and could be studied with a landscape ecology approach: therefore, we can introduce a 'peninsular biogeographic theory applied to inland peninsular-shaped ecosystems' analogously to 'island biogeography theory applied to mainland'.

The Italian peninsula shows a wide latitudinal range, a collocation in a specific Mediterranean scenario, a peculiar orographic pattern represented from Apennines (role as longitudinal 'bridge' and as trasversal 'barrier'). These specific features, analogously to others present in some peninsulas (e.g., 'Everglades' in Florida, 'Central desert' in Baja California), affect the diversity patterns in many taxa, assemblages and single species.

Peninsular data could be utilized in multiscale conservation strategies (from landscape to regional level) and this issue could be related to applied biogeography, other than to the descriptive and causal biogeography.

INTRODUCTION

The analysis of distribution patterns of the species and groups and their causal processes appears the main research focus in macroecology and biogeography (e.g., from Wallace, 1876). 'Peninsula effect' (Simpson, 1964) is a widely studied issue.

Although individual peninsulas were deeply studied (e.g., Wiggins, 1999), a general review has never been published. The aim of this work is to provide a general arrangement on this topic, reviewing the literature on peninsular patterns, on their causal processes for specific assemblages and taxa, and debating the role of data-set for conservation and planning strategies. A particular discussion was developed about the Italian peninsula, emphasizing their features and the role of Apennines as bridge and/or barrier in determining the observed diversity patterns.

PATTERNS OF DIVERSITY AND THE LATITUDINAL GRADIENT OF SPECIES RICHNESS

Many patterns and gradients of biological diversity, organized in time and space, are known in biogeography. Among them we can include the species-area relationship, the latitudinal, altitudinal, and productivity gradients, the Rapoport's rule (mean range size gradient), the habitat complexity theory and the intermediate disturbance patterns (Preston, 1962; Rapoport, 1982; Hobbs and Huenneke, 1992; Willig et al., 2003).

Three main hypotheses have been proposed to explain the observed patterns of diversity: 1) the species-area relationship, which implies that species richness increases as a power function of surface area; 2) the species-energy hypothesis, which predicts that species richness will be positively correlated with the available energy; 3) the historical hypothesis, which explains diversity gradients by the patterns of recolonization/extinction after historical events (e.g., glaciations, sea level oscillations with consequent isolation or creation of land bridges), genetic differentiation and speciation (Willig et al., 2003).

The latitudinal gradient of species richness is a general negative relationship between latitude and species richness, with a peak in richness at the equator. This pattern has been observed in many taxa, in marine and continental ecosystems, throughout the hemispheres (Fisher, 1960; Pianka, 1966; Kiester, 1971; Schall and Pianka, 1978; France, 1992; Rosenzweig, 1992; Willig et al., 2003). Many theories have been proposed to explain these latitudinal gradients of species richness and the analysis of the causes has received much speculation and debate (Pianka, 1966; Willig et al., 2003); nevertheless, recently no single theory is widely accepted for the overall taxa investigated (Rosenzweig, 1992).

Towards the equator, communities will contain more species because of the climatic stability, a greater range of resources and an increase of primary productivity, a higher specialization with a species overlapping in use of the resources. In this sense, latitude is a useful surrogate measure that integrates day length and climatic variables (that influence the productivity), the habitat complexity and resources (e.g., Newton and Dale, 1996). Many hypotheses highlight the role of biotic interactions (competition, species packing,

coevolution and speciation, resource partitioning; France, 1992). These factors, and the linked changes along a North-South gradient, could strongly influence the latitudinal species diversity. In these studies, species diversity was widely considered synonym of species richness, corresponding to the γ -(regional) diversity (Whittaker, 1977; Magurran, 2004).

If at global scale the climatic factor (and their components, e.g., stability, yearly range of temperature, mean annual rainfall) is the most widely accepted basic explanatory hypothesis of the latitudinal gradient; at less wide continental/regional scale, topographic heterogeneity, altitudinal range, and a corresponding change in habitat diversity, was indicated to explain the species richness gradient (e.g., Enge, 1997 and reference therein). Finally, at local scale, many other recent factors could contribute or confound the observed latitudinal patterns of diversity (environmental heterogeneity, patchiness, and anthropogenic landscape fragmentation, disturbance and productivity patterns, local topography and oro-geography). Following Lambshoad (2002), two linked ecological processes should control the patterns of biological diversity in space: 1) disturbance and, 2) productivity that determine habitat diversity (i.e., patchiness and environmental heterogeneity; Tews et al., 2004) and, consequently, the spatial species diversity patterns.

THE PENINSULA EFFECT: HISTORICAL-DISCIPLINARY ARRANGEMENT

Global latitudinal pattern of species richness shows anomalies at lower scale (regional or local; e.g., the 'isthmus effect': Robinson et al., 2000). Among them, peninsular-shaped geographic areas received much attention.

In peninsular Florida, Robertson (1955) documented a decreasing number of bird species richness within habitats, progressively farther from North to South; Duellman and Schwartz (1958) observed an anomalous decline in the number of native amphibian and reptile species. In the Sixty's, Simpson (1964), investigating the distribution of mammal species of North America, observed a decline in species richness from the base to the tip of some peninsulas (Baja California, Florida, Labrador, Alaska, New Scotland). He named this local anomalous gradient as "peninsula(r) effect": i.e. a reduction of species diversity along the peninsulas, more evident when comparing this parameter versus equally-sized mainland regions. MacArthur and Wilson (1967) and Cook (1969) corroborated the existence of this pattern in landbirds of the largest North American peninsulas (e.g., Florida, Baja California).

'Simpsonian peninsular effect hypothesis' (hereafter, SPH) explains the observed patterns in terms of extinction/immigration dynamics related to the theory of insular biogeography (hereafter, TIB): peninsular geometry may act to hinder immigration and increase extinction acting on observed species

richness patterns (Simpson, 1964; MacArthur and Wilson, 1967). Following this hypothesis, peninsulas were considered “semi-insulae” where immigration of individuals could proceed from only one direction (i.e., from their base).

In the Seventy's, Taylor and Regal (1978) supported the SPH for six vertebrate groups (lizards, snakes, birds, mammals in general, heteromyd rodents, bats) that showed a base-tip distribution pattern in Baja California peninsula. Many criticisms developed in the Eighty's, especially on the causal factors or processes driving the observed patterns. In Baja California peninsula, Seib (1980) highlighted as lizards and snakes showed a dual pattern: species with a northern origin decreased in richness towards South, inversely to species with a southern origin. He highlights as ecological and historical deterministic factors appear to explain better the patterns in respect to SPH (for a historical review of debate on Baja California patterns, see Murphy, 1990). Nevertheless, Taylor and Regal (1980), replying to Seib (1980), defended the SPH. Gilpin (1981) and Lawlor (1983) pointed out as the immigration and extinction processes in Baja California peninsula might be responsible of only a small proportion of the species and, utilizing more complete data set, observed that only a specific taxa (heteromyd rodents), among those analysed by Taylor and Regal (1978), showed a decreasing gradient towards South (i.e., towards the tip of this peninsula).

Consequently, a debate arisen regarding: 1) the effective existence of base-tip taxon-(or guild)-specific patterns and 2) the individuation of factors/processes as causal predictors explaining these patterns.

In many case studies, ‘peninsula effect’ was utilized as a term regarding either a pattern or a factor/process explaining it. Lawlor (1983) assumed that the “peninsula effect”, as pattern, could not be a general property among vertebrates. Taylor and Pfannmuller (1981) concluded that the peninsula effect, as pattern, could be observed only in specific geographic circumstances and taxa (or ecological guilds). They assumed that factors/processes, other than equilibrium dynamics (e.g., linked to SPH), could influence or determine the observed patterns.

Taylor (1987) implemented the SPH with a model considering the over-water immigration of individuals towards peninsulas from other continental areas. In taxa characterized by high vagility and dispersal rate (e.g., migrant butterflies, bats, birds), dispersal over water could exceed dispersal over land (i.e., from the base of peninsulas), therefore altering the peninsular patterns. Following this approach, three main causal variables should be considered to explain observed peninsular patterns: peninsular geometry, orientation in respect to “mainland” and taxa-specific dispersal capacity. Moreover Taylor highlighted as in peninsulas with low angle in respect to neighbouring mainland, active dispersal could be more effective than passive one (Taylor, 1987).

Many authors studied patterns in different taxa at various spatial scales; birds and, among invertebrates, butterflies (especially in North American peninsulas) were the more studied groups in classical 'geographic/oceanic' peninsulas at regional scale (see below; Tab. I and Tab. II).

Tab. I - Reviewed papers on 'Peninsula effect' (1950-2005; n = 84). Only the works that explicitate selected parameters, scale, patterns and causal factors/processes are reported. Parameters: S: include the following acceptions: 'species richness', 'species density', 'species diversity' (community/assemblages level), Ab: abundance (species level); type = peninsular type: g: 'oceanic/geographic' peninsula; i: 'habitat/inland' peninsulas. Scale (peninsular size): l = local (about 1-100 km wide), r = regional (about 100-1000 km), c = continental (>1000 km). Pattern: b-t = selected parameter decrease base-tip; t-b = decrease tip-base, N-S: decrease towards South, S-N: decrease towards North, E-W: decrease towards West, i-e: decrease interior-edge, m: minimum in the middle of the peninsular body; M: maximum in the middle. Causal factors/processes: SPH: Simpsonian peninsular hypothesis; E: ecology sensu lato (C: climate; V: vegetation; HD: habitat diversity and complexity; HT: habitat turnover; CO: competition); O: orography (PG: peninsular geometry; GE: geography; AR: area effect); H: history (P: paleogeography; PC: paleoclimate; S: speciation; G: glaciations); A: anthropization (postpleistocenic and recent); B: biogeographic processes sensu lato (LG: linked to latitudinal gradient) (*segue*).

study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Caporaiacco, 1950	scorpions	S	Italy	g	r	b-t	E, H (P, S)
Robertson, 1955	birds	S	Florida	g	r	b-t	E, H (G)
Duellman and Schwartz, 1958	herpetofauna	S	Florida	g	r	b-t	A
Simpson, 1964	mammals	S	Baja California, Florida, Labrador, Alaska, New Scorialand	g	r	b-t	SPH
MacArthur and Wilson, 1967	landbirds	S	Florida, Baja California, Yucatan	g	r	b-t	SPH
Zangheri, 1968	macrolepidoptera	S	Europe (and Italy)	g	r	latitudinal continental gradient (N-S; tip of Palearctic)	B (LG)
Cook, 1969	birds	S	4 North American peninsulas	g	r	b-t	H (P, G)
Rohwer and Woolfenden, 1969	birds	S	Florida	g	r	b-t	E, S (G)
Kiester, 1971	herpetofauna	S	Florida	g	r	b-t	no evident explanation (see Means and Simberloff, 1987)
Robertson and Kushlan, 1974	birds	S	Florida	g	r	b-t	H (extinction and disequilibrium); E (pattern N-S in habitat availability)
Tramer, 1974	birds	S	North American peninsulas	g	r/c	b-t	SPH?

Tab. I - Reviewed papers on 'Peninsula effect' (1950-2005; n = 84) (*segue*).

study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Slud, 1976	bird	passerine/ non passerine ratio	Neotropics (Florida, Yucatan)	g	r	lower ratio in peninsulas	E, O (patterns in physical environmental complexity)
Schall and Pianka, 1977	herpetofauna	S	Iberia	g	r	b-t (amphibians); r-b (reptiles)	C (high latitudinal range); E
Emlen, 1978 (cit. in Todd, 1993)	birds	S	Florida	g	r	b-t	E
Taylor and Regal, 1978	lizards, snakes, birds, mammals (total), heteromyd rodents, bats	S	Baja California	g	r	b-t (more evident in heteromyd rodents; not evident in snakes)	C-V gradient
Wamer, 1978	resident birds	S	Florida	g	r	b-t	HD (pattern b-t)
Blondel, 1979	birds	Ab	Europe	g	c	E-W	B (E, H)
Lee, 1980	herpetofauna	S	Yucatan	g	r	m; no latitudinal effect, no reduction towards tip	E, HD, H (endemism pattern due to Pleistocenic isolation)
Seib, 1980	reptiles	S	Baja California	g	r	no general trend (turnover northern/ southern species)	E (HT, CO); H (tropical species extended their range following past climatic oscillation)
Feoli and Lagonegro, 1982	flora	S	Italy	g	r	M	O, C, HD, SPH?
Massa, 1982	landbirds, Hymenoptera Formicidae, Coleoptera Carabidae, Cicindelidae, Chrysomelidae, Idroadephaga, Scarabeoideae Pleurosticta + Pachypodidae	S	Italy	g	r	b-t; endemism: r-b	PG, C, V, O (decreasing altitude towards tip)
Taylor and Pfanmuller, 1982	small mammals; ground beetles	S	Manitoba peninsula (Lake Winnipegosis), Canada	g	l	no general pattern	E (dispersal: pattern due to over-water dispersal)
Lawlor, 1983	mammals	S	Baja California	g	r	b-t but lower compared with Taylor and Regal (1978) data (pattern only on 4 species in respect to 18)	H, E (habitat availability), more the equilibrium (SPH)

Tab. I - Reviewed papers on 'Peninsula effect' (1950-2005; n = 84) (*segue*).

study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Murphy, 1983	herpetofauna	S	Baja California	g	r	different patterns in ecological characterized groups	H (evolution from isolation); E (abiotic factors, C, predation)
Winemiller, 1983	freshwater fish	S	Corcovado park, Osa peninsula, Costa Rica	g	l	b-t	E (productivity patterns)
Busack and Hedges, 1984	lizards, snakes	S	Florida, Iberia, Yucatan, Baja California	g	r	b-t (Florida); m (Yucatan); no evident pattern (Baja California, Iberia)	Florida (PC, E; habitat availability); Iberia: H (no saturation in species, O as barriers, isolation in Miocene); Iberia, Yucatan, Baja California: H; PC (Pleistocenic changes, isolation, endemism pattern), E
Contoli et al., 1985	trophic system <i>Tyto alba</i> -micromammals	trophic system parameters	Italy	g	r	functional trophic system pattern	E, H, A
Racheli and Zilli, 1985	lepidoptera	S and single species distribution analysis	Italy	g	r	complex pattern (e.g., temperate: b-t)	E, H (plio-pleistocene), dispersal (Apennine effect)
Due and Polis, 1986	scorpions	S	Baja California	g	r	b-t; M	turnover in habitat structure (E, P)
Milne and Forman, 1986	wood plants	S	Maine (US)	g	l	b-t; i-e (coastal)	HD pattern
Brown, 1987	lepidoptera	S	Baja California	g	r	b-t; m	H, E, no SPH
Haila et al., 1987	conifer forest birds	S	Western Palearctic taiga	i	c	N-S	CO, SPH (insular biogeography)
Means and Simberloff, 1987	herpetofauna	S	Florida	g	r	b-t	E (habitat availability; Everglades effect (low topographic diversity; range contraction for decrease in habitat availability)
Raivio, 1988	birds	S, Ab	Hanko peninsula (Southern Finland)	g	l	no significant differences in richness base-tip	HD, E

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study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Schwartz, 1988	woody species	S	Florida, Aleutine (Alaska), Seward (Alaska)	g	r	Florida: no evident gradient; t-b, m, tropical species: t-b, temperate species: b-t; Alaska (Aleutine and Seward): b-t	Florida: C more the H (palinological data); Alaska: low change in C and O along base-tip, AE (no decrease in richness if control area factor); Aleutine: AE, HD; Seward: AE
Auth, 1989	amphibians, turtles, lizards, snakes	S	Florida	g	r	b-t	E, HD (reduction towards tip); H (last 40,000 years)
Brown and Donahae, 1989	lepidoptera Sphingidae	S	Baja California	g	r	b-t	H (isolation), E
Rousseau and Keen, 1989	mollusca	S	Western Europe	i	c	E-W	peninsular effect (continental scale), SPH, E, B (range termini)
Brown and Opler, 1990	lepidoptera	S	Florida	g	r	temperate: b-t; tropical: t-b; pattern not uniform nor consistent	E, C
Martin and Gurrea, 1990	lepidoptera	S	Iberia	g	r	b-t (complex)	E, O, H
Murphy, 1990	herpetofauna	S	Baja California	g	r	dual patterns (dispersers towards N, towards S)	paleogeographic causes
Contoli, 1991	trophic system <i>Tyto alba</i> -micromammals	trophic system parameters	Italy	g	r	functional trophic system pattern	E, H, A
Maher, 1992	Florida panther (<i>Felis concolor coryi</i>)	population parameters	Florida	g	r	b-t (abundance, populaton parameters)	insularization (genetic, demographic causes)
Massa, 1993	breeding birds	S and single species distribution analysis	Italy	g	r	b-t	H (Mediterranean refuges)
Engstrom, 1993	birds	S	Florida	g	r	b-t (abundance, population parameters)	E, H, A (forest fragmentation, disturbance patterns, SPH?)
Tellería and Santos, 1994	insectivorous passerines	Ab	Iberia	g	r	b-t	C, H, A

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study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Battisti and Contoli, 1995	breeding landbirds	S	Italy	g	r	b-t	O, C, HD, SPH?
Garcia-Ocejo and Gurrea, 1995	Coleoptera Crisomelidae	S	Iberia (Sierra de Guadarrama)	g	l/r	b-t	P
Barbosa and Benzal, 1996	small mammals	diversity parameters from Barn Owl pellets	Iberia	g	r	b-t	HD
Bardi et al., 1996	vertebrates	S	Italy	g	r	b-t	A, E, O
Contoli and Penko, 1996	rodents	S	Italy	g	r	b-t	HD, A (habitat fragmentation)
Lobinske et al., 1996	Diptera Chironomidae	S	Florida	g	r	b-t	abiotic factors (water availability pattern)
Silva, 1996	birds	S	Brazil	i	l/r	b-t	edge and landscape effects
Tackaberry and Kellman, 1996	trees	S	Belize-Venezuela	i	l	no evident pattern	AE (controlling area, no evident effect base-tip)
Battisti et al., 1997	terrestrial micromammals	community parameters	Italy and Salento subpeninsula	g	r	absence of species in Salento	E, H, A
Brichetti, 1997	birds	S (chorological categories)	Italy	g	r	b-t: palearctic; t-b: Mediterranean	C, E
Enge, 1997	herpetofauna	S	Florida	g	r	b-t	O, E, landscape factors; H (ecological events in the last 40,000 years determine distribution)
Oberdorff et al., 1997	freshwater fish	S	North America and Europe	i	c	no evident patterns	orientation rivers, AE, E (more important than H)
Sosa-Escalante et al., 1997	terrestrial mammals	S and other parameters	NE Yucatan	g	r	complex pattern	HD and C
Capizzi and Riga, 1998	communities preyed by <i>Asio otus</i>	S	Italy	g	r	b-t	E
Cagnin et al., 1998	small mammals	community parameters	Italy and Iberia	g	r	b-t (and other patterns)	O, E, C
Contoli, 1998	small mammals	S, diversity index, evenness	Italy	g	r	richness: b-t; evenness: t-b	E, H

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study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Kremen et al., 1998	birds, primates, small mammals, butterflies, cicindelids, scarabeid beetles	S, β -diversity	Masoala peninsula (Madagascar)	g	l	b-t (prevalent pattern)	E (environmental gradients)
Thiollay, 1998	raptor communities	S	Peninsular Malaysia and large islands of South-East Asia	g	r	b-t	species area requirements, H, A (forest fragmentation)
Vargas et al., 1998	freshwater fish and amphibian (endemic and indigenous)	S	Iberia	g	r	endemic: t-b; amphibians: two biogeographic regions	freshwater fish: LG (P events of the Upper Oligocene-Lower Miocene). Amphibians: C, P; dispersal factors linked to C, P
Battisti and Contoli, 1999	breeding birds	mean range size	Italy	g	r	b-t	O, C, HD, SPH?
UCL, 1999	birds	S	France	i	r	decrease NE-SW with areas that deviate from model (Pirenees, Alps, Mediterranean areas)	O (pattern), C (pattern), continental (interior) vs. coastal (edge) pattern (increase?), A (habitat fragmentation)
Wiggins, 1999	landbirds	S	Baja California	g	r	decrease base-middle, increase middle to tip	concave diversity gradient of montane species (E); limited immigration (no SPH)
Kocher and Williams, 2000	butterflies	S	some North American peninsulas (not specificate)	g	c/t	lat continental pattern; fail in NA peninsulas	general factors: E, A (habitat disturbance), geography
Riddle et al., 2000	mammals, birds, amphibians, reptiles	genetic level	Baja California	g	r	filogeographic pattern	H (P)
Baquero and Tellería, 2001	mammals	S, rarity, endemicity	Europe and Southern mediterranean peninsulas	i	c	large scale peninsular effect (continental scale): richness patterns: b-t; abundance: Palearctic species b-t, endemics and rares: t-b	H (Mediterranean peninsulas as refuge areas), E
Battisti and Testi 2001	breeding birds	S	Italy	g	r	b-t	O, C, E
Cho et al., 2001	plant species	S	Korea	i	l	b-t	edge effect

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study	taxa/assemblages	parameter	study area	type	scale	pattern	causal factors
Harrison et al., 2002	exotic plants (6 species)	Ab	North America	i	l	3 species on 6: b-t	E (habitat suitability)
Johnson and Ward, 2002	Hymenoptera Formicidae	S (species and genus level)	Baja California	g	r	b-t at species level no at genus level	H (range disjunction), E (HD, O: elevation range); when minimizing habitat effects no evident pattern is present
Arrigoni, 2003	Amphibians anuran	S	Yucatan	g	r	b-t (negative relation latitude-richness)	C (e.g., pluviometric regime)
Battisti and Testi, 2003	breeding birds	S (chorological categories)	Italy	g	r	different patterns for different chorological groups	C, H
Carrascal and Diaz, 2003	forest breeding birds	S	Iberia	g	r	b-t (european species); t-b (mediterranean species)	O, C (as patterns), E (autoecology at species level), B (abundance centre)
Galarza and Telleria, 2003	wintering passerines	S, Ab	Iberia	g	r	E-W	peninsula effect sensu lato
Choi, 2004	lepidoptera	S	South Korea	g	r	b-t	HD, PG (peninsular orientation)
Adrianjakarivelo et al., 2005	small mammals	S	Masoala peninsula (Madagascar)	g	l	b-t	E, SPH
Kocher and Williams, 2005	lepidoptera	S	Baja California, Florida	g	r	b-t	O (topographic pattern)
Peck et al., 2005	carabid beetles	S	Florida	g	r	b-t; endemisms: M; tropical species: t-b	H, E (isolation, Tertiary, Quaternary, sea level oscillation, dispersal over water)
Tubelis, 2005a	birds	S, Ab	Australia	inland	l	b-t (species-specific responses); abundance	home range higher: decrease in abundance, AE, edge effect

Tab. II - Geographic peninsulas and taxa/assemblages studied. Only papers concerning 'oceanic/geographic' peninsulas at regional scale were considered (see caption Tab. I).

geographic peninsulas	flora	invertebrates	fish	herpetofauna	birds	mammals	total
Florida	1	4		6	8	1	20
Baja California		5		6	4	4	19
Yucatan				3	1	1	5
Iberia		2	1	3	4	2	12
Italy	1	3			6	4	14
Korea	1	1					2
Labrador						1	1
Alaska <i>s.l.</i>						1	1
Alaska Aleutine	1						1
Alaska Seward	1						1
New Scotland						1	1
Malaysia					1		1
North American peninsulas indet.		1			2		3
total	5	16	1	18	26	15	81

Large-scale peninsula effect was observed in Western Europe, considered as a macropeninsula of Eurasia (Haila et al., 1987; Baquero and Tellería, 2001). Baquero and Tellería (2001) observed, at continental scale, anomalous distribution patterns of mammals in Mediterranean peninsulas and islands. Peninsula effect was observed also in marine areas (peninsular-shaped sea floor, Norwegian sea; Lambshoad, 2002).

These studies evidenced a progressive criticism against the SPH as the only causal factors/process explaining the peninsular patterns (Lawlor, 1983; Busack and Hedges, 1984; Due and Polis, 1986; Means and Simberloff, 1987; Schwartz, 1988) and many other causal factors/processes were proposed adapted to different geographic contexts, scales and taxa or ecological groups (Means and Simberloff, 1987). Moreover, other analyses were carried out on taxonomic groups and on phenological, chorological, ecological-based assemblages (e.g., migrants vs. sedentaries, Mediterranean vs. temperate species). At species level, either genetic or demographic patterns were investigated in this sense (e.g., Maher, 1992; Riddle et al., 2000; Tab. I).

Peninsula effect appeared to be not a general pattern, but an occasional phenomenon shown in some taxa and assemblages in specific contexts (Means

and Simberloff, 1987). In some peninsulas different taxa might show different patterns or similar base-tip gradients induced by different causes (equilibrium theory related, historical, ecological, anthropogenic) in different contexts. Consequently, characterization of selected scales, contexts and assemblages studied (e.g., if taxonomic, ecological, chorological or phenological) play a role in determine patterns and processes (Due and Polis, 1986; Means and Simberloff, 1987; Brown and Opler, 1990).

Absence of evident gradients along the axis of peninsulas were considered a “peninsula effect” by Schwartz (1988), who did not observe a reduction in woody flora richness from North to South Florida. Indeed, also this pattern could correspond to a peninsular effect because it is in contrast with the expected increase of species number towards the tropics (latitudinal gradient; Schall and Pianka, 1977; Willig et al., 2003).

CAUSAL FACTORS AND PROCESSES OF PENINSULAR PATTERNS

An analysis of a wide literature on this issue (n = 84 papers; Tab. I) achieved the specification of different causal factors that might explain the diversity patterns. They could be reconducted to the following main groups:

Recent stochastic factors/processes (equilibrium and derived island biogeography theories; SPH)

Immigration-extinction dynamics could be observed in peninsular populations at the border of their range: e.g., the decreased rate of immigration and increased rate of extinction towards the tip of the Florida peninsula was discussed by Robertson (1955), Simpson (1964), MacArthur and Wilson (1967), Cook (1969), Kiester (1971). Brown and Opler (1990) highlighted as the immigration-extinction dynamics could contribute to the observed patterns in addition to others causal factors (e.g., ecological *sensu lato* and historical-paleogeographic).

Area effect ('per se' and 'as gradient')

In peninsulas that decrease their available area towards the tip, the occurring number of species could decrease, in this direction, with available area. Many peninsulas reduce their area towards the tip (e.g., Italian peninsula, Aleutian and Seward peninsulas in Alaska). Consequently, an area effect on the species (*sensu* Preston, 1962) could be expected: i.e., when species richness is normalized to area (e.g., species density: n. species/area; log-transformed, Massa, 1982) the trend base – tip tends to disappear (Massa, 1982; Battisti and Testi, 2001 for Italy; Schwartz, 1988 for Alaskan peninsulas). Therefore, in many study cases,

peninsular effect as pattern of decreasing species number with proximity to the tip is a result of reduced area (Australian Heritage Commission Act, 1999).

In regard to the equilibrium theory, an analysis species-area (see Magurran, 2004) could be carried out in peninsulas. The availability of habitat area for specific taxa could be lower in respect to the mainland or could decrease along a base-tip peninsular gradient (e.g., in Italy, Calabria and Salento subpeninsulas in respect to peninsular main body; Contoli e Penko, 1996, Contoli, 2004). Further research are requested on this issue.

Isolation effect

The tip of the peninsulas are more distant from source populations of specific taxa that are widely diffused in non-peninsular mainland (see the “Center of origin” theory; Brown, 1988, and the ‘abundance centre’ hypothesis in Sagarin and Gaines, 2002). An isolation for distance (or caused from orthogonal barriers in respect to the axis of peninsulas) could act on populations distributed along the peninsular body, with a progressive reduction of the immigration rate, a reduction of individual abundance in isolated populations, and an increase of their extinction rate. This could imply a decrease in richness towards the tip of the peninsulas. This model assumes that an increase of distance from a distribution centre (i.e., the centre of a species range) implies a lower abundance and, consequently, fewer opportunities for immigration (Schwartz, 1988).

Applying the TIB to the mainland (Diamond, 1975), the z values in power function species/area (Preston, 1962; MacArthur and Wilson, 1967), a taxa-specific coefficient related to isolation degree of an ‘archipelago’, should be intermediate between 0.17 and 0.35 (range corresponding to ‘isolated systems’: MacArthur and Wilson, 1967; Watling and Donnelly, 2006). Nevertheless, Busack and Hedges (1984) demonstrated that for a set of peninsulas and taxa the obtained z values are not different in respect to mainland areas, so not supporting the TIB applied to mainland peninsulas (Simpson, 1964).

Supporting the SPH, Tellería and Santos (1993) observed as some forest species could experiment source/sink dynamics with sink population and low densities in extreme South of Iberian peninsula where their habitat are extremely dispersed and fragmented other than distant from the center of the specific range. In butterflies of Florida, where the temporary occurrence of host plants permits the colonization of ephemeral populations, unsuitable temperatures and extinction of host plant populations induce local extinctions in perypheral populations, with source-sink dynamics (Brown and Opler, 1990). Many “northern” and/or forest bird species show their range termini progressively towards the tip of the peninsulas with North-South axis. In the boundaries of the distribution ranges the abundance is lower than in core areas for autoecological

causes (resource availability, competition; Brown, 1984). Carrascal and Diaz (2003) suggesting that the Iberian peninsular general patterns of birds could be related to the distribution of single forest bird species, that progressively become extinct towards South. This single-species phenomenon could influence the patterns at higher guild or community level.

Isolation for distance or due to barriers along the peninsulas could influence the genetic diversity at single species level, with a differentiation or speciation of more isolated populations and with consequences at species richness level and of their relative spatial patterns. These events could mask the equilibrium dynamics (Riddle et al., 2000; see below: 'historical event').

Historical events as paleoclimatic oscillations, paleogeographic and tectonic changes ('diversity disequilibrium models'; Schwartz, 1988)

These factors/processes could determine turnover in species assemblages, genetic differentiation in newly isolated populations, speciations. These events could intervene on diversity patterns in peninsulas that, consequently, might not show clear base-tip gradient (e.g., Busack and Hedges, 1984), or could evidence contra-trends and anomalous patterns (e.g., more richness in the tip due to a higher number of endemisms; maximum/minimum values in middle side of the peninsular body, differently to expected from the SPH model). In Baja California, during the Miocene and Pliocene, the Cape Region (on the peninsular tip) was isolated from Mexico and Northern California. Consequently, barriers to dispersal arised differentiating many species with speciation events (see the 'transgulfian vicariant species': Murphy, 1990; Riddle et al., 2000). Isolation and change of ecological conditions induced by paleogeographic events produced a high rate of subspeciation for mammals in South Florida (Layne, 1984). Peck et al. (2005) showed a pick of endemic species richness of Coleoptera Carabidae in the middle of Florida, as a possible reflection of Tertiary and Quaternary islands as centers of isolations and speciation. General pattern of richness in this group was influenced also from over-water dispersal between Florida and West Indies when in the Pleistocene the sea level was lower (Peck et al., 2005).

Endemism and vicariance, due to paleotectonic barriers, appear to contribute to some peninsular patterns in scorpions of Baja California peninsula. Due and Polis (1986) observed that endemisms were 10-15 % higher in number in respect to non peninsular areas due to a paleogeographic isolation from Mexico.

In some taxa with limited dispersal capacity, fossils and palinological records support the historical (paleoclimatic and paleotectonic) events as the main factors that explain the actual peninsular patterns (Busack and Hedges, 1984). Murphy (1990) evidenced as causal factors of distributional patterns are deterministic

(non random) and linked to paleogeographic events, differently to stochastic processes, as extinction and recolonization, linked to the SPH.

Some philogeographic patterns observed in specific assemblages of species are due to paleogeographic events (for Baja California, see Riddle et al., 2000).

Pleistocenic glaciations are presumable responsible of the actual diversity patterns of some vertebrates (e.g., mammals) in Europe: in Quaternary the southern Mediterranean peninsulas hosted hot-spots of species richness, rarity and endemism (Vargas et al., 1998; Baquero and Tellería, 2001). These could explain the actual peninsular patterns of species in some groups: sea oscillations and glaciations with landbridges were suggested as the main causal factors, other than ecological ones, responsible of many range disjunction in Lepidoptera pattern in Italy (Racheli and Zilli, 1985).

Recent (deterministic) factors/processes (ecology, climate, geography)

An actualistic approach supports the idea that observed patterns of taxa in peninsulas merely reflect actual (i.e., postpleistocenic) patterns of habitat diversity, heterogeneity and patchiness, climatic regime, flora and vegetation structure, resource availability and biological processes (Busack and Hedges, 1984; Milne and Forman, 1986; Raivio, 1988). Further recent geographic features (surface area, collocation, orientation, latitudinal range), could be added to ecological s.l. factors. The presence of a decreasing number of species towards the peninsular tips does not necessarily result from extinction/recolonization processes (SPH) or from historical events, but could be a consequence of base-tip gradients in above mentioned recent ecological s.l. and geophysical factors (Taylor and Regal, 1978; Seib, 1980; Lawlor, 1983; Enge, 1997).

Climate (as gradient)

Present climatic regime, linked to geometry and topography of peninsulas, influences a plethora of ecological factors. In peninsulas with a relatively high latitudinal range (e.g., Florida, Baja California, Italian and Iberian peninsulas) a strong gradient in climate induces a progressive or abrupt turnover in flora, vegetation, resources and fauna (Raivio, 1988; Brown and Opler, 1990; Carrascal and Díaz, 2003).

Patterns of many habitat types show a base-tip gradient, especially in North-South oriented peninsulas with a wide climatic range. These patterns could influence distribution of richness and abundance in many species and groups (e.g., Raivio, 1988). Changes of extreme temperatures along a gradient is likely the more important factor that explains the distribution pattern in Florida's herpetofauna (Enge, 1997). Climate, vegetation and topography are

the most important features affecting avian species in Baja California (Wiggins, 1999). The reduction towards South of xeric and temperate habitat induces a decrease of habitat-related species in Florida's herpetofauna (Means and Simberloff, 1987).

At single species level, in Iberian peninsula, Tellería and Santos (1993, 1994) showed that some species of Palearctic, highly diffused, forest Passeriformes reduced their density from North towards South as consequence of the reduction in ecological habitat availability for climatic causes; vice versa some Mediterranean species decreased their abundance towards North. Consequently, patterns at species level could influence patterns of species richness at assemblage level. Changes on vegetation features along the Florida peninsula, induced by climatic gradient, are the main causal factor that determines the species pattern in climate-related assemblages (Wamer, 1978; Schwartz, 1988). In Italy the higher variability of vegetation develops along a mainly North-South direction (Blasi et al., 2006).

Ecological-climatic gradients are responsible of many species richness gradient, also opposite to the classical base-tip decreasing patterns, observed especially in assemblages of climate-characterized species. For instance, in North-South oriented peninsulas (e.g., Baja California; Italian peninsula, Florida), inverse peninsular patterns (i.e., decreasing species richness from tip to base) were observed in woody flora (Schwartz, 1988), carabid beetles (Peck et al., 2005), butterflies (Brown and Opler, 1990), northern and southern disperser species among reptiles (Seib, 1980; Murphy, 1990), forest birds (Carrascal and Diaz, 2003), and breeding birds (Brichetti, 1997; Battisti and Testi, 2003), when they were subdivided in chorological assemblages or ecologically (related to climate) groups (e.g., temperate vs. tropical species; Mediterranean vs. European species; see also Seib, 1980; Brown, 1988). In Italy, butterfly distribution pattern was influenced from the wide range in North-South direction of the peninsula which comprise two floristic regions (Racheli and Zilli, 1985). Turnover in species from base to tip in North-South oriented peninsulas is responsible of some observed general patterns (Due and Polis, 1986).

Geographical position has a significant effect on forest bird species (Holarctic, Palearctic, Euroturkestan, and European species), being related positively with latitude in Spain (Carrascal and Diaz, 2003): latitude (as expression of climate) has a negative and prominent role in determining richness in Mediterranean bird species and those widely distributed in Africa (for Italy: Battisti and Testi, 2003).

Peninsulas with no evident abiotic and/or climatic changes (e.g., with narrow latitudinal range or not North-South oriented) did not show species turnovers (e.g., Alaskan peninsulas; Schwartz, 1988 and the "habitat change model").

In peninsulas oriented with the tip towards North, decreasing base-tip diversity patterns could be coherent with the global latitudinal gradient. In Yucatan peninsula, differences may be associated with the increase of precipitation towards South (ecological-climatic factor at global scale) also if a reduced immigration towards the tip (North) of peninsula of the poor disperser species may exacerbate the (base-tip) latitudinal gradient (Lee, 1980, 1993).

Ecology sensu lato - Ecological complexity and environmental heterogeneity (as gradient)

In Iberian peninsula, Purroy (1988) observed that the factors that determine abundance and diversity of wintering bird peninsular assemblages are geographical, topographical and ecological ones (see also Tellería and Santos, 1994). In butterfly of Florida, the food plant requirements and seasonal dispersal patterns of the species explain the observed diversity patterns (Brown and Opler, 1990).

In birds, an increase of species richness in a site can be expected increasing the structural complexity of the ecosystems and the primary productivity (MacArthur, 1964). The peninsular tip could show topographic and ecological simplification, so inducing changes in resource availability and in species richness. Ecological simplification may induce changes in structure of species assemblages in peninsulas: in Yucatan peninsula tropical birds show lowering in the passerines/not passerines ratio in respect to the mainland (Slud, 1976).

The “environmental heterogeneity hypothesis” (Milne and Forman, 1986) might be responsible in peninsulas of the deviation from the SPH model, due to direct correlation between habitat diversity (i.e., environmental heterogeneity; Tews et al., 2004) and species richness, especially at local/landscape scale. At genus level, Johnson and Ward (2002) did not show a decrease towards the tip of Baja California in the ants, when minimizing habitat diversity effects. In three North American small peninsulas (Maine), Milne and Forman (1986) highlighted as differences in species richness were due to environmental differences along a base-tip gradient.

Topographic heterogeneity (e.g., elevation range, geomorphological diversity) influences the habitat diversity and resource availability at landscape/regional scale (Tews et al., 2004): in a small peninsula of the Madagascar, differences in species richness are ascribable above all to ecological differences and to local topography along a base-tip gradient (Adrianjakarivelo et al., 2005). Elevation range is correlated with habitat diversity because variation in elevation provides different climatic, edaphic and vegetational conditions (Kocher and Williams, 2000). Habitat diversity, consequently to topographic heterogeneity and elevation range, explains the peninsular pattern in butterflies of South

Korean peninsula (Choi, 2004), in herpetofauna through Florida (Means and Simberloff, 1987), in ant species richness in Baja California (Johnson and Ward, 2002) and in butterflies in North American peninsulas (Kocher and Williams, 2000).

In any case, in peninsulas, environmental heterogeneity (and relatively linked patterns) could vary; 1) with a patchy pattern (no relation with the collocation along the peninsula); 2) along a base-tip gradient; 3) along a coastal edge-interior patterns; 4) with mixed patterns: this may affect the diversity patterns.

Anthropic factors (habitat fragmentation and disturbances as gradient)

If the anthropical impact is peninsular-oriented (i.e., with a base-tip gradient of impact) this could induce a corresponding gradient of anthropical disturbance (recent and historical, since about 10,000 years ago; Covas and Blondel, 1998) that could influence the peninsular species richness patterns. Deforestation, fires, pasture and others anthropogenic disturbances in Mediterranean peninsulas influence the patterns in many species and groups (Enge, 1997; Covas and Blondel, 1998). Particularly, human-induced habitat heterogeneity and fragmentation might act increasing or decreasing the total species richness, due, respectively, to progressive extinctions of sensitive species and an increase of anthropophilous generalist species (Saunders et al., 1991; Andr n, 1994; Fahrig, 1997; Battisti, 2003; Battisti, 2004). At fine-grained scale, disturbances and habitat fragmentation induce a reduction in species richness (in peninsular Florida herpetofauna; Means and Simberloff, 1987; Enge, 1997) and in other parameters (e.g., bird biomass; Lebreton and Ledant, 1980). Anthropization has been also compared to a historical disequilibrium (Brown and Opler, 1990).

Multiple factors

Multiple factors could be combined in explaining peninsular patterns for specific taxonomic groups (Teller a and Santos, 1993) and some causal factors or processes could mask others (Means and Simberloff, 1986; Raivio, 1988; Wiggins, 1999). Consequently, could be difficult to separate single factors in explains the patterns: e.g., Feoli and Lagonegro (1982) observed in Italy a maximum of flora species richness in the middle of the peninsula due to complex historical, topographic (high elevation range) and ecological factors (see also Contoli, 2000; Contoli, 2004). Moreover, diversity patterns at larger global scale, as latitudinal gradient of species richness, could interfere with the local peninsular patterns making difficult the analyses of the causal factors (Willig et al., 2003).

PENINSULAR PATTERN ANALYSIS: METHODS AND LIMITATIONS

Different methods were used to investigate the peninsular pattern of species diversity (Tab. III). Methodological problems were stressed by many authors and are here reported.

Tab. III - Methods utilized to investigate the peninsular patterns of species diversity and relative references.

Method	References
abrupt comparison from base to tip	e.g., Taylor and Regal 1978; Wiggins, 1999.
analysis of peninsular distribution of range termini	e.g., Means and Simberloff, 1987; Schwartz, 1988.
subdivision of the peninsulas in latitudinal bands	e.g., Schwartz, 1988; Murphy, 1990; Battisti and Contoli, 1999; UCL, 1999; Wiggins, 1999; Battisti and Testi, 2001; Johnson and Ward, 2002; Battisti and Testi, 2003; Peck et al., 2005.
cells at landscape scale (inside a grid in a peninsular study area)	Schall and Pianka, 1977; Busack and Hedges, 1984; Cho et al., 2001; Carrascal and Diaz, 2003; Choi, 2004.
comparisons with records at different latitude	from field studies or collections: e.g., Taylor and Regal, 1978; Haila et al., 1987; Tellería and Santos, 1993 (abundance data); Battisti et al., 1997; Oberdorff et al., 1997; Riddle et al., 2000; Johnson and Ward, 2002.
comparisons with records at different sites along gradients	landscape scale: e.g., Winemiller, 1983; Andrianjakarivelo et al., 2005.
points along peninsular-shaped patches	e.g., Raivio, 1988; Tubelis, 2005.
comparisons among records included in geographic or political units	e.g., Lebreton and Ledant, 1980; Bardi et al., 1996; Vargas et al., 1998.
orthogonal bands along the main peninsular axis	e.g., Schwartz, 1988; Brown and Opler, 1990; Battisti and Contoli, 1995; Contoli, 2000.
comparisons peninsular <i>vs.</i> continental data	e.g., Slud, 1976; Rousseau and Keen, 1989; Newton and Dale, 1996; Baquero and Tellería, 2001.
revisions and comparisons	e.g., Enge, 1997; Wiggins, 1999; Engstrom, 2000.

Definition of the peninsular range, scales, and procedure of data setting

Raivio (1988) and Schwartz (1988) highlighted as the subjective procedure of define the beginning of the peninsulas and to set the relative data might mask the effective patterns and their causal factors/processes. Moreover, cells in the borders of the peninsula include the sea, so influencing the available area and species richness: therefore a normalization of the values relative to coastal cells is necessary (Raivio, 1988; Battisti and Contoli, 1997; Contoli and Penko, 1994).

Scale utilized could imply different causal factors/processes. When deciding the area of the cells and/or the latitudinal band range, the size and dispersal ability of the organisms studied have to be considered; indeed, peninsular size and dispersal capacity of the target taxa could affect the patterns (Raivio, 1988). In this sense, for each study, different and multiscale subdivision are requested.

Lack of data

Lack of data or inadequate sampling are further extrinsic factors that might influence the real pattern of species diversity, inducing to erroneous conclusions (Taylor and Regal, 1978; Seib, 1980; UCL, 1999; McCain, 2003). In many cases, data on target taxa (e.g., Atlas data) or assemblages are incomplete and could intervene in the definition of peninsular patterns (Racheli and Zilli, 1985; McCain, 2003). Data set obtained in recent surveys at national scale are incomplete for many groups and lack of knowledge may be responsible of the observed patterns (e.g., Ruffo e Stoch, 2005; Stoch, 2006): e.g., in Italian breeding birds Atlas lack of data is higher in Southern regions, so emphasizing the North-South (i.e., base-tip) gradient in peninsular decrease of species richness (Meschini and Frugis, 1993; Battisti and Contoli, 2001).

Taxonomic problems

Taxonomic problems may contribute to generate anomalous patterns in diversity: e.g., the inverse peninsular patterns observed in snakes of Baja California by Seib (1980; increase towards the tip) could be due to inclusion, in the analysed groups, of morphological variants considered as different species, so inflating species richness in the tip and obtaining biased patterns (Murphy, 1990).

Qualitative vs. quantitative data

In peninsular studies, analyses focused on qualitative data (e.g., presence/absence of the species) or quantitative ones (e.g., abundance): different implications arise from the two approaches (Raivio, 1988).

Hierarchic level of diversity

A cautionary approach is requested when comparing data from cells or bands (comprising sectors at regional/landscape scale) or, on the contrary, from single ecosystem/fragments. Indeed, the observed species richness could be due to different basic causal factors. Murphy (1990), criticizing Seib (1990), proposed to compare wide bands instead of records from sample points: indeed, using specific locality records we compare the presence/absence in habitat patches

(α -diversity level) more than latitudinal differences at γ -diversity level (*sensu* Whittaker, 1977; Magurran, 2004).

Comparing diversity data at regional/landscape scale (e.g., utilizing wide cells) we compare diversity at γ -level. Therefore, observed patterns in peninsulas are patterns in γ -diversity. In this sense, heterogeneity at landscape scale could act in defining the level of richness in bands or cells, so masking extinction/immigration dynamics (SPH), if existing. Contrary, an approach at single fragment level (i.e., comparing a set of fragments along a peninsular gradient relative to specific habitat type) correspond to a α -level approach. In this sense, comparing species diversity at α -level (fragment scale) we could evidence richness patterns relative to insular/peninsular biogeographic patterns (SPH). This two approaches are conceptually different and different implications in terms of causal processes can arise. For instance, many distributional records of snakes of Baja California peninsula do not accurately reflect the latitudinal base-tip occurrences but rather the presence/absence from specific habitat patches that could induce different implications (Murphy, 1990). Nevertheless, analyses for latitudinal bands are at coarse-grained scale and fine-grained events at patch-scale (as, e.g., extinction and recolonization at metapopulation level), could be neglected with an approach at γ -level. Moreover, in these analyses could prevail deterministic macroscale events (paleogeographic and ecological as well as heterogeneity patterns: γ -level) in respect to stochastic microscale (landscape) events (e.g., SPH patterns; α -level).

'GEOGRAPHIC/OCEANIC' AND 'HABITAT/INLAND' PENINSULAS

Few studies have examined the peninsula effect in places (and scales) other than in geographical *sensu stricto* peninsulas. Since Taylor and Regal (1978), peninsulas were considered also in ecological acception (patches of peninsular-shaped habitat inside a different landscape matrix: Silva, 1996; Tackaberry and Kellman, 1996; Harrison et al., 2002; Tubelis, 2005a; Tubelis, 2005b; see also Bennett, 1999). In this sense, Tackaberry and Kellman (1996) and Silva (1996) distinguish between 'geographic/oceanic' and 'habitat/inland' peninsulas. "Habitat/inland" peninsulas generally develop on scale in time and space of two or three order of magnitude lower than continental ones. Nevertheless, the spatial scale approach is not a good criterion for grouping the two types: many geographic peninsulas are of small size (1-100 km; van Riper III, 1982; Winemiller, 1983; Milne and Forman, 1986; Raivio, 1988) and 'habitat/inland' peninsulas in mainland could be very extended (e.g., tropical forest in Brazilian savannah; Silva, 1996). In any case, if the shape is the same (i.e., "peninsular"), causal processes, implications and disciplines that analyze this issue could be different between 'geographic/oceanic' and 'habitat/inland' peninsulas (Tab. IV).

Tab. IV - Disciplines related to the different peninsular types ('oceanic/geographic vs. 'habitat/inland' peninsulas).

'geographic/oceanic' peninsulas	'habitat/inland' peninsulas
Insular biogeography	Landscape ecology
Historical and ecological biogeography	Metapopulation ecology
Macroecology	Population genetic
Population genetic (differentiation; speciation)	Landscape conservation
Regional conservation	Environmental planning
	Nature reserve and ecological network planning

We can introduce a 'peninsular biogeographic theory applied to inland peninsular-shaped ecosystems' analogously to 'island biogeography theory applied to mainland' (i.e., island-shaped fragment or nature reserves in the mainland; Diamond, 1975; Burkey, 1989). In any cases, habitat ecosystems (peninsular- or insular-shaped) are embedded in a landscape matrix of different type inside the mainland, differently from the classical theories (peninsular and insular), where the sea is the 'matrix' surrounding the lands (islands and peninsulas *sensu stricto*; Simpson, 1964; MacArthur and Wilson, 1967).

In landscape ecology, the peninsular shape of a remnant patch suggest many implications: e.g., edge effect may be stronger in the tip, in respect to the base of "peninsulas". Recent acquisitions in landscape ecology, conservation biology and wildlife management suggest as the edge effect is the main threat for populations and communities isolated in remnant patches embedded in anthropized matrices (Laurance and Yensen, 1991; Soulé and Orians, 2001). The reduction in available habitat-area and in interior habitat-area, the increase in edge area (e.g., increase of influence of the surrounding matrix), progressively higher towards the tip along peninsular-shaped patches, are the major causal factors that explain the observed patterns (Tubelis, 2005a; Tubelis, 2005b). Many studies in fragmented landscapes were carried out, emphasizing the role of size area, isolation and edge effect at different ecological level (Simberloff and Abele, 1976; Saunders et al., 1991; Andrén, 1994; Fahrig, 1997). In peninsulas, the edge/interior area ratio is higher in respect to non-peninsular shaped habitat inducing a higher edge effect. Consequently, many authors suggest that circular reserves should be preferred to thin, elongated or "peninsular shaped" ones (e.g., Tackaberry and Kellman, 1996; Bennett, 1999). Machtans et al. (1996) supported this hypothesis: if source areas of specific populations have a peninsular shape, these populations could be reduced in number and dispersal can be negatively influenced. Moreover, dispersal from the core sectors is insufficient for balancing extinctions in the tip of peninsular patches (Diamond, 1975).

Baz and García-Boyeró (1995) highlight as rounded rather than long, thin or peninsular-shaped fragments are advantageous for the maintenance of butterfly diversity. Supporting it, Silva (1996) analyzed the forest bird communities in riparian forest peninsular-shaped in Brazilian savannah; Tackaberry and Kellman (1996) studied the tree species richness in tropical riparian forest elongated as peninsulas; Harrison et al. (2002) analyzed the distribution and abundance of exotic plants along roads in a peninsular nature reserve; Cho et al. (2001) showed, in a peninsular shape reserve of Korea, as the reduction in tree layer and herbaceous layer species richness was related to the loss of interior habitats and increase of edge effect towards the tip. Tubelis (2005a) highlights as richness and abundance of birds in peninsular-shaped *Eucalyptus* forest patches of Australia decrease in the tip, observing that reduction in area and distance from interior/core sectors could interfere on foraging dynamics and home ranges of the individuals, especially in large birds. Diamond and May (1976) suggest as populations inside strictly and elongated reserves show extinction rates higher if compared to circular ones. This is linked to edge effect induced by matrix (see van Riper III, 1982). However, many authors have criticized these assumptions (Simberloff and Abele, 1982; Means and Simberloff, 1987; Raivio, 1988).

'PENINSULA EFFECT' AND ITALIAN PENINSULA

In Italian peninsula, 'Peninsula effect' is a widely studied issue. Research focused prevalently on two terrestrial taxonomic groups: arthropoda (especially insecta) and vertebrates (especially birds and mammals).

Artropoda

Among invertebrates and at continental scale, Zangheri (1968) observed an increase of macroLepidoptera richness from northern Europe towards the Mediterranean region. At less wide scale, Caporiacco (1950) supposed that the distribution of scorpions in Italy depends from ecological constraints rather than from an insufficient recolonization from northern populations after extinction in the South. In Eighty's, Massa (1982) observed as some taxa of invertebrate (Hymenoptera Formicidae, Coleoptera Carabidae, Cicindelidae, Chrysomelidae, Hydroadephaga, Scarabeoidea Pleurosticta and Pachypodidae) show a gradient of fauna exhaustion from North to South in peninsular Italy. In Lepidoptera, Racheli and Zilli (1985) showed a rarefaction towards North of the 'Southern' species, present only in xerothermic refuges. They highlighted as Italian peninsula was characterized by a high homogeneity with a low faunistic diversification. This high similarity among different sectors of the peninsula could be due to a 'bridge effect' of the Apennines (Zilli and Racheli, 1985). The development in

an approximately North-South direction of the peninsula, different from other Mediterranean peninsulas (Iberia and Anatolia), and the wide extension (about 10° of latitudinal range), could facilitate a strong climatic turnover of the species with different ecological requirements (thermophilous vs. mesophilous) and a consequent base-tip patterns. Many populations are situated in extreme border of the European range of the species, so showing high probability of extinction in short time for environmental, genetic, demographic causes (see 'S.O.S. populations' in Rapoport, 1982). Racheli and Zilli (1985) pointed out as there are problems for an application of the SPH for the Italian Lepidoptera. Indeed, two strong assumptions of the SPH model (1: source populations and origin of the dispersal at the base of peninsula; 2: homogeneous climatic, topographic and ecological characteristics from North to South) are not observable in Italian peninsula where a strong heterogeneity of ecological constraints and a latitudinal (climatic) gradient is present from base to peninsular tip. Moreover, historical factors acted confounding the patterns: during the glacial period many population drifted their source population southward in the Mediterranean refuge and then dispersed towards North (Racheli and Zilli, 1985).

More than immigration/extinction dynamics, also occurring in many species, general pattern of Lepidoptera in Italian peninsula could be explained from dynamics linked to Terziary and Quaternary bridges and from high range of variation of climatic features (La Greca, 1984). Further factors as competition among species in Mediterranean areas (e.g., among European vs. Mediterranean vicariants) could intervene in the observed patterns (La Greca, 1984; La Greca, 1990). Finally, in the last 10,000 years, human induced disturbances and habitat transformations, especially in Southern zones induced a decrease or a turnover in species richness (Covas and Blondel, 1998). Many of these disturbances fragmented many ecosystem types along the Italian peninsula and this is responsible of disjunct distribution patterns of many butterfly species at national scale (Racheli and Zilli, 1985).

Evolutionary factors (e.g., genetic differentiation) is another factor complicating the patterns (Racheli and Zilli, 1985). Morphogenetic evidences inside some species (divergences) and absence of species from suitable areas support these hypotheses (La Greca, 1984; 1990). Therefore, historical (last Cenozoic and Pleistocene), ecological (climate, competition) and anthropical factors (disturbances, habitat fragmentation) may be the cause of the present patterns in several taxa (Racheli and Zilli, 1985).

Vertebrates

Yet Lebreton and Ledant (1980), at wider scale, showed a peninsular pattern at continental scale, e.g., a North - South gradient in the landbird of Mediterranean

area. Mediterranean peninsulas and, among them, the Italian peninsula, are situated also in the extreme tip of the Eurasian region where an E-W decreasing gradient of species richness was observed (Massa, 1993).

Italian vertebrates were widely studied in this topic. An analysis of latitudinal gradient of the species along the Italian peninsula was carried out by Massa (1982) on landbirds that showed a North-South gradient of species richness. A low species density (calculated as species number/area, log-transformed ratio) was observed in Southern Italy and Sicily. Orography (e.g., decreasing pattern in altitudinal range towards South), peninsular geometry (e.g., strictly and elongated shape of Italy with reduction of area towards South), bioclimatic (vegetational) differences were identified as main causal factors of the observed patterns and two thresholds (at level of Tuscany and the Naples-Gargano line) were recognized (Massa, 1982).

An evident decrease in species richness from North to South was reported from the national breeding birds atlas and comparing several regional birds atlases among them (Massa, 1993; Boano et al., 1995). This was confirmed southward in the Italian peninsula utilizing breeding birds atlas at national scale and clustering the data in latitudinal bands (Battisti and Contoli, 1997; Battisti and Contoli, 1999). Such a gradient was slightly different in various ecological and phenological categories (Battisti and Testi, 2003). Anomalies of the general trends (e.g., peak in richness) appear to reflect orographical variations along the peninsula. In this sense, species richness appears to be affected by orophysiographical, bioclimatic, environmental and anthropical factors which overlap the strictly historical (paleoclimatic, paleogeographic) ones (Battisti and Testi, 2001).

Massa (1993) suggested that the actual pattern of landbird assemblages was influenced from the last glacial period: e.g., many forest species show a relic distribution in Southern Italy where this area represented a refuge in the glacial period (18-13,000 y.a.). Successively, anthropic disturbances in the last interglacial was considered a factor inducing changes at species and assemblages level. The “protostoric revolution” with annexes disturbances (fires, pasture, agriculture, deforestation) created macroscopic changes in vegetation in a subsequent period (xerothermic period: 8-4,000 y.a.). Extensive changes in species distribution induced changes also in the overall patterns in specific taxa and assemblages: e.g., deforestation and development of maquis vegetation favoured the expansion towards North of the Mediterranean bird species (Massa, 1993).

At level of assemblages of chorologically-characterized bird species, Bricchetti (1997) and Battisti and Testi (2003) showed an increase of Mediterranean species and a reduction of Palearctic species from North to South along the Italian peninsula that could affect the general peninsular diversity pattern.

At species level, many evidences in landbirds highlight the effect of the high latitudinal range of the Italian peninsula. Among them, *Passer italiae* (Vieillot, 1817) and *Passer hispaniolensis* (Temminck, 1820) show a morphometric

differentiation along the peninsula (Massa, 1993; Fulgione and Milone, 1998). In the Pleistocene (10,000 y.a.), *Passer domesticus* (Linnaeus, 1758) spread towards South along anthropical corridors. Clinal North-South variations are known also for *Parus caeruleus* Linnaeus, 1758 (Massa, 1993), and probably many Eurosibiric and European species that show a relic distribution along the Apennines show a genetic differentiation in respect to European population or have probably sink populations along the Apennines, increasing towards the peninsular tip: e.g., *Aquila chrysaetos* (Linnaeus, 1758) (Massa and Ingegnoli, 1993). A genetic ecological differentiation arisen in some forest bird species (Massa, 1993) and, among these, some are subspecies of conservation concern (Bulgarini et al., 1998).

Recently, many bird species have experienced an expansion towards South along the Italian peninsula, colonizing many areas in some decades, along a base-tip gradient: e.g., *Streptopelia decaocto* (Frigalszky, 1838) and *Sturnus vulgaris* Linnaeus, 1758. Intrinsic evolutive changes and extrinsic factors, as anthropization, could have promoted this range expansion (Fasola and Brichetti, 1993; Massa, 1993).

Among mammals, some groups show analogous North/South (base-tip) patterns. Geomorphology at landscape scale, geographic features, ecological constraints, and human disturbances, subdivide the rodent fauna of Italy in four peninsular regions (North, South, Calabria and Salento; Contoli, 2000). Rodents show a decrease of species number towards South. Salento and Calabria subpeninsulas, in the tip of the Italian peninsular body, show qualitative differences in species assemblages, with Calabria more rich than Salento subpeninsula (Contoli and Penko, 1996; Battisti et al., 1997). Geomorphology, isolation effect, anthropization, and fine-grained patchiness, progressively higher towards the South of the peninsula, were identified as causal factors of the rodents peninsular patterns (Contoli, 1991; Contoli and Penko, 1996). At community level, species richness is higher in Northern Italy, evenness is higher in Southern; between the two Italian subpeninsulas, diversity is higher in Calabrian subpeninsula compared to Salento (Contoli and Penko, 1994; Contoli, 1998; see the γ -diversity analysis in Contoli, 2004).

Differences between North and South Italy were observed also at trophic level in the "*Tyto alba*-small mammals" trophic systems: peninsular regions (Apulia, Calabria, Campania) did not host many rare species of Insectivora and Rodentia, and these regions show a trophic similarity with the insular ones (Contoli et al., 1985). Capizzi and Riga (1998) observed in the diet of a Strigiformes, *Asio otus* (Linnaeus, 1758), an increase of taxonomic diversity of the preys with the latitude. Peninsular biocoenosis of small mammals appear to be mainly influenced from extinction/immigration dynamics, in many cases linked to historical anthropization and to the presence of barriers (sea, orography), differently from continental ones where recent ecological factors were identified as the main causal factors (Contoli et al., 1985).

Italian and Iberian peninsulas show an impoverishment of small mammal species richness towards the tip and, when compared, their total abundance is higher in the Iberian peninsula in respect to the Italian one (Cagnin et al., 1998). Paleoclimate and historical geological factors were identified as factors affecting of these patterns. The shape of mountain chains in Iberia is relatively orthogonal in respect to peninsular axis and to NE-SW dispersal routes, differently from Apennines in Italy, that could play a role of bridge in short and long term dynamics (see also Baldaccini, 1993). A bridge effect of the Apennines was hypothesized in many vertebrate groups (e.g., migrants birds: Baldaccini, 1993; large mammals: Lovari, 1993). Many mesophilous and forest species (e.g., *Sorex* spp., *Myodes glareolus* (Schreber, 1880)) utilize the Apennines as dispersal route towards South, therefore affecting the general patterns in species assemblages (Cagnin et al., 1998).

Local extinctions or genetic differentiation (e.g., endemism) is more probable for Iberian populations of small mammals than Italian ones, due to these orographic barriers. However, a role of the reduction of genetic flow due to the wide latitudinal extension of the Italian peninsula was hypothesized to influence size and habitus of two sympatric species of *Apodemus* in forest habitats (Panzironi et al., 1994).

Present factors (altitudinal range, climate, resource availability) could be added to explain the patterns of richness and abundance, different in two peninsulas (Cagnin et al., 1998): e.g., in Iberia, latitude (indirectly as climate) could explain the differences in abundance of small mammals from North to South (Barbosa and Benzal, 1996), whereas in Italian peninsula the restricted differences in altitudinal range and climate between North and South were considered the causes of the absence of a pattern in total abundance of the species (Cagnin et al., 1998). Biotic factors, as competition, can arise: for example, the decrease of Insectivora/Rodentia ratio towards South should be correlate with a trophic competition with Lacertidae (Cagnin et al., 1998; Contoli et al., 2000a, 2000b).

Other than a 'bridge effect', Apennines in peninsular Italy could induce isolation, for example, because of orographic interruptions to North-South peninsular axis: e.g., in Irpinia/Daunia (Campania-Apulia) and in Southern Apennines. Thresholds in patterns are evident in Irpinia and along the Southern Apennines (Calabria and Basilicata show a lower altitudinal range and a higher habitat fragmentation at landscape scale due to anthropization and disturbance than in adjacent regions; Bologna, 1997; Battisti and Testi, 2001). South of the line Naples-Gargano, Apennines massifs are isolated from the northernmost ones and this imply evident changes in fauna and flora distribution and composition. Although the number of endemic species (vertebrates, vascular plants) is higher in Central and Southern Apennines, various taxa show in Southern Italy a lower species richness (Bardi et al., 1996).

Many works emphasise the role of the Apennines as a faunistic 'bridge' in peninsular Italy (Ruffo, 1959; Massa, 1982; Battisti and Contoli, 1997; La Greca,

1963; Cagnin et al., 1998). Battisti and Testi (2003) observed an oscillation in the β -turnover index in breeding bird species due to orographic features. In this sense, Apennines appear the peculiarity of Italian peninsula that drive the observed patterns, analogously to specific local features observed in others peninsulas: in Florida, the 'Everglades effect' (Means and Simberloff, 1987); in Baja California, the ecological and orographic effect linked to the central desert (Due and Polis, 1986; Wiggins, 1999); in the Iberian peninsula the effect linked with the development of the orographic systems in an East-West direction (Cagnin et al., 1998).

IMPLICATION FOR PLANNING AND CONSERVATION

Continental/regional scale

Analysis of diversity patterns in space is useful to focus on areas of conservation concern: these areas might be characterized by high species richness ('hot spots') or by a high number of species of ecological concern and of endemic and genetically differentiated forms (Boitani et al., 2003; Maiorano et al., 2006).

Abrupt threshold in species richness and species turnover, as observed by β -diversity analyses, suggests the presence of barriers (ecological and/or anthropogenic) or historical events that produce them (Battisti and Testi, 2003). β -diversity analyses are useful to individuate changes in patterns and abrupt thresholds at different scale (Koleff et al., 2003). Species turnover originated from natural patchiness or from human-induced fragmentation leads to different implications and the derived patterns should be analysed in a different way: conservation strategies should distinguish carefully this different turnover types.

Analogously to latitudinal gradient at global scale, some conservation considerations can be carried out in peninsulas. For a group that experiences a decrease of species richness towards the tip, different strategies could be promoted focusing, e.g., at level of hot-spots in the base (more richness at community level) and at species level in the tip, where richness is lower but genetic differentiation could act. Populations in the tip, isolated for peninsular distance or orthogonal barriers, could be characterized as sink or genetically differentiated, so requiring specific conservation strategies (e.g., in red lists: Bulgarini et al., 1998; see also Rapoport, 1982).

Diversity patterns are also useful to address strategies for protected area systems. For specific contexts with high species richness, conservationists should favour the size of nature reserves, in contexts with higher evenness should favour the number of them (Contoli, 1991). In Italy, analysis of trophic system "Strigiformes-small mammals" highlights as in Northern Italy, the strategies could favour the conservation of large areas, because they host rich communities (high γ -diversity), whereas in Southern Italy could favour the number of nature reserve in respect to their size area, because of the general higher heterogeneity and species turnover at landscape scale (high β -diversity; Contoli, 1998).

The peculiarity of Italian peninsula (wide latitudinal range; collocation in a Mediterranean scenario, peripheral to Palearctic continental area, specific orographic pattern represented from Apennines), stimulate a definition to appropriate strategy where the peninsular-linked factors are preminent in a general arrangement. In Italy there are two opposite patterns in many groups: a North-South gradient of decreasing species richness (especially Palearctic and temperate species) and a North - South gradients of increasing endemic species (Stoch and Vigna Taglianti, 2005), following analogous patterns at continental European scale (e.g., Baquero and Tellería, 2001). This suggest selective strategies addressed to focus on species richness in the North, and on rarity and endemism in Southern Italy. At species level, the wide latitudinal range of Italian peninsula could induce source/sink gradients along the base-tip axis with conservation implications in specific taxa (genetic differentiation, demographic patterns).

On 'habitat/inland' peninsulas we can refer to disciplinary debate on nature reserve design and ecological network planning (i.e., a planning strategy with the aim to mitigate the habitat fragmentation process and edge effect; Romano et al., 1999; Romano, 2000; Battisti, 2003). In this sense, landscape ecology attempt to provide a strong conceptual framework to study the effect of the peculiar shape of inland peninsulas, the progressively reduction in area towards their tip, the increase of isolation (for barriers or for distance) and the role of landscape matrix surrounding the peninsular-shaped ecosystems (Forman and Godron, 1981; Simberloff, 1988; Farina, 2001; Tubelis, 2005a).

For Italy, further research could investigate thresholds and trends in many other groups where data at national scale are available, following a peninsular biogeographic approach (e.g., invertebrate groups: Ruffo and Stoch, 2005). Comparisons among effective vs. potential data (acquired with a probabilistic or deterministic approach) could reveal an interest: e.g., comparing the Italian ecological network data (Boitani et al., 2003) vs. atlas data known for specific taxa. For Italy, many thematic territorial layers and data bank are available at national scale (bioclimate, flora, vegetation, fauna, habitat fragmentation, land cover use and land cover change, biopermeability: e.g., Tomaselli et al., 1973; Pedrotti, 1991; Properzi et al., 1998; Romano, 2000; Boitani et al., 2003; Conti et al., 2005; Blasi et al., 2005; Ruffo and Stoch, 2005; Scoppola and Blasi, 2005; Blasi et al., 2006) that could be compared with the distribution of many ecological-related groups. This could allow an analysis of causal factors affecting the observed patterns. In this sense, could be useful carried out area-species analyses on specific focal habitat types along the peninsular axis to evaluate the role of SPH on selected assemblages.

Assemblages could be investigated at taxonomic level or to ecological, phenological, chorological ones. Patterns of specific ecological-characterized assemblages along the peninsular gradient, linked to specific habitat type, could be useful to test eventually the SPH, also if more precise demographic data could

be requested, other than spatial ones. European and “northern” species linked to mesophilous forest types could experiment a progressive rarefaction due to longer distance for their centre of origin (Brown, 1988), so hypothesizing source-sink patterns and extinction/immigration dynamics towards the tip of the peninsulas.

Many other questions could be developed. Among them: orographic-induced thresholds in species richness (e.g., at level of Irpinia/Daunia) are observed for different taxa? β -turnover analyses for several groups confirm a general model along the Italian peninsula or the patterns are group-specific? Diversity patterns are correlated to relative vagility of the assemblages studied? Among the causal factors/processes (SPH, ecology, orography, history, anthropization, mixed), there are main predictors for specific taxa or groups?

Peninsula effect and related patterns and processes is a issue strongly linked to selected contexts, scales, ecological/taxonomic levels (e.g., if species, taxa or ecological and chorological assemblages differently characterized). The theoretical background and the observed empiric patterns could be acquired in planning and conservation sciences other than in the classic biogeography. In this sense, this disciplinary sector could be considered an issues also related to applied biogeography (Spellerberg and Sawyer, 1999).

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