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HETEROTOPY REMASTERED WITH A QUANTITATIVE TOOL: THE CASE STUDY OF EUROPEAN BEECH (*FAGUS SYLVATICA* L. SUBSP. *SYLVATICA*) IN PENINSULAR ITALY AND SICILY

Abstract - *Heterotopy remastered with a quantitative tool: the case study of European beech (Fagus sylvatica L. subsp. sylvatica) in peninsular Italy and Sicily.* The term "heterotopic" was applied to phytogeography referring to those populations found on soils apparently different from those typically occurring across the distribution range of a given species. In Italy, it was also applied to European beech populations generally occurring at an altitude below 800 m a.s.l. Based on a multivariate analysis using climatic and altitudinal data, we propose a method to apply reliably this concept to the European beech occurring in peninsular Italy and Sicily. Our results suggest that beech populations located at an altitude ≤ 600 m a.s.l. can be defined as "quantitatively heterotopic" in Italy. These populations mainly occur on the Tyrrhenian side, marked by high oceanicity. Most of them are located outside of the natural vegetation series with European beech and, some are more than 20 km outside. Our method could be applied to other species in order to quantify the level of heterotopy by defining *ad hoc* thresholds, resulting from multivariate analysis.

Keywords - Climate, phytogeography, Apennine, altitudinal range

Riassunto - *Eterotopia rivisitata tramite analisi quantitative: il caso studio del faggio (Fagus sylvatica L. subsp. sylvatica) in Italia peninsulare e Sicilia.* Il termine "eterotopico" è stato inizialmente applicato in fitogeografia per riferirsi a quelle popolazioni che crescono su suoli differenti dal contesto tipico per una determinata specie. In Italia questo concetto è stato applicato a quelle faggete che crescono generalmente al di sotto degli 800 metri di altitudine. Sulla base di un'analisi multivariata di dati climatici e altitudinali, proponiamo un metodo per testare l'applicabilità di questo concetto nelle faggete dell'Italia peninsulare e della Sicilia. I nostri risultati suggeriscono di definire come "quantitativamente eterotopiche" quelle popolazioni di faggio che in Italia sono localizzate ad un'altitudine ≤ 600 m s.l.m. Queste popolazioni sono principalmente concentrate sul versante tirrenico caratterizzato da una marcata oceanicità. Molte di queste popolazioni sono inoltre localizzate al di fuori della serie naturale di vegetazione con faggio e fra queste, alcune sono distanti più di 20 km da tali serie. Il metodo qui utilizzato potrebbe essere applicato ad altre specie per quantificare il livello di eterotopia, definendo delle soglie limite sulla base dei risultati dell'analisi multivariata.

Parole chiave - Clima, fitogeografia, Appennino, range altitudinale

Introduction

The term "heterotopic" (from the Greek roots "*hetero-*" meaning "other" + "*topos*" meaning "place" = other place) was used for the first time in biology by Haeckel (1866) to define a change in germ-layer origin of reproductive organs in animals. Later, it was used in phytogeography by Jackson (1900), referring to those populations found on soils differing from those typically occurring across the distribution range of a given species, and by Kraus (1911), referring to calciphile plants growing on non-calcareous soils, and vice versa. In Italy, Pampanini & Negri (1928) were likely the first authors to introduce this term for European beech (*Fagus sylvatica* L. subsp. *sylvatica*) populations occurring at low altitude (150-400 m a.s.l.). Since then, most of the Italian authors used "heterotopic" referring to beech or other populations of woody species, such as *Taxus baccata* L. (De Dominicis, 1969), *Picea abies* (L.) H. Karst (Magini, 1972) or *Quercus ilex* L. (Viciani *et al.* 2004), occurring outside their common altitudinal range or, in a broader sense, not growing within their typical macroclimatic context. In Italy, also some populations of non-woody species were termed as heterotopic, e.g. *Cardamine chelidonia* L. and *Lolium giganteum* (L.) Darbysh. in the valley of the Lente River (Viciani *et al.*, 2004), *Veratrum album* L. in the province of Brescia (Crescini, 1986), *Luzula nivea* (L.) DC., *Nardus stricta* L., *Senecio ovatus* (G.Gaertn., B.Mey. & Scherb.) Willd. subsp. *alpestris* (Gaudin) Herborg in the Groane Regional Park (Gariboldi *et al.*, 2007), or even subalpine and alpine plants reported by Prosser & Festi (1990) at low altitudes in Trentino-Alto Adige. In Italy, the European beech populations occurring below 800 m a.s.l. have been generally considered as heterotopic (Pignatti, 1994), even though in some cases stands above 800 m a.s.l. were also considered heterotopic (e.g. Hofmann, 1961; Sabbatini *et al.*, 2011). No objective criteria have been agreed upon to use this term in a consistent way, independent on the individual author's opinion.

The Apennines population of European beech are of particular interest because they are the only populations with a documented uninterrupted presence since the middle Pleistocene (Follieri *et al.*, 1988; Magri, 1998). Particularly, among these populations, those located at low altitude represented both refugial areas during the last glacial period, and privileged lo-

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cations during interglacials (Magri, 1998, 2008). Accordingly, we have selected the European beech in peninsular Italy and Sicily as an ideal case study to quantify and standardize the 'heterotopy' concept.

Materials & Methods

Study species

Fagus sylvatica L. subsp. *sylvatica* is the most abundant broad-leaved tree in central Europe and in many mountain systems of southern Europe. Italy hosts its southernmost populations (Jalas & Suominen, 1976), which occur over several phytoclimatic regions, from the Mediterranean to the Eurosiberian regions (Pignatti, 1998). Climate differs considerably between the high-mountain stands in the Alps, where trees are subjected to cold winters and no water stress during the growing season, and those in the Apennines, characterized by summer water stress and cold spells in the spring (Di Filippo *et al*., 2012). Concerning the altitudinal range in Italy, it spans from 200-400 to 2000-2100 m a.s.l. in the central and southern Apennines (Filibeck *et al*., 2015), whereas the optimal elevation range is located between 900 and 1900 m a.s.l. (Pignatti, 1998; Cutini & Di Pietro, 2006).

Source of data and statistical analysis

We performed an extensive bibliographic research in order to detect references of 'heterotopic' (or similar terms, such as 'extra-zonal') populations of *Fagus sylvatica* in Apennines and Sicily. Accordingly, we found 19 references (Tab. 1, Fig. 1a) reporting 113 populations. Our analysis was strictly applied to beech populations, and no records of isolated trees were considered in the present work. In this way, we also avoided to include cultivated trees in the analysis. Beech populations were georeferenced using a GIS software (QGIS 2.18) and, when authors indicated an altitudinal range for a beech forest, we used the mean value. In addition, we randomly generated 305 control points, falling within the polygons of potential natural vegetation including *F. sylvatica*, ensuring at least one point in each polygon (Fig. 1b). For the definition of potential natural vegetation, see Tuxen (1956). Polygons of potential natural vegetation of our target species were provided by http://www.va.minambiente.it/ (see also Blasi *et al*., 2004). Each control point and putatively heterotopic stand was associated with environmental variables, selected according to their potential biological relevance for the distribution of *F. sylvatica*. The following bioclimatic variables, together with elevation data (Digital Elevation Model) at 30 arc-seconds

Table 1. Bibliographic references of heterotopic beech populations, ordered from northern to southern Italian regions.

Number of georeferenced points	Italian region	Altitudinal range	Reference
2	Emilia Romagna	155–595	De Curtis *et al.*, 2014
1	Tuscany	200	Pampanini & Negri, 1928
1	Tuscany	300	Chiarugi, 1930
15	Tuscany	450–800	Negri, 1930
5	Tuscany	310–540	Padula, 1956
1	Tuscany	800	Frassineti & Bottacci, 1997
4	Tuscany	410–510	Cavalli & Drosera, 1999
1	Tuscany	600–800	Foggi *et al.*, 2000
1	Tuscany	300–400	Viciani *et al.*, 2004
1	Tuscany	345–385	Landi *et al.*, 2009
24	Tuscany	420–1095	Sabbatini *et al.*, 2011
11	Tuscany	330–900	Leonardi *et al.*, 2012
5	Marche	262–415	Elisei, 2015
1	Lazio	550–650	Montelucci, 1956
16	Lazio	310–735	Anzalone, 1961a; 1961b
14	Lazio	300–550	Scoppola & Caporali, 1996
6	Campania/Calabria	410–750	Agostini, 1971
5	Puglia	285–980	Hoffman, 1961

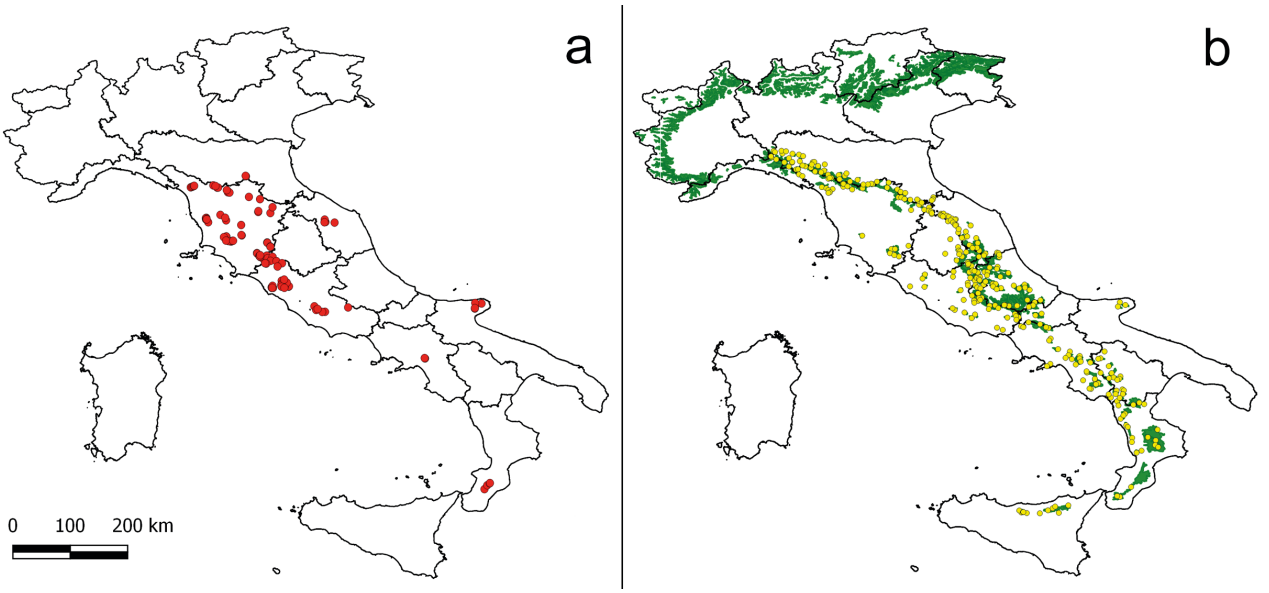

Figure 1. Distribution in peninsular Italy of putatively 'heterotopic' beech populations as reported in literature (a), and of 305 randomly generated control points (yellow) within the potential natural vegetation including *F. sylvatica* (green) (b).

(about 1 km^2) of spatial resolution grid, were obtained from the WorldClim data set (http://www.worldclim.org): annual mean temperature (BIO01); temperature seasonality (BIO04); temperature annual range (i.e., continentality, BIO07); annual precipitation (BIO12); precipitation seasonality (BIO15). These climatic variables, along with elevation, are the most useful factors to define the eco-physiological tolerance of a species (Hijmans & Graham, 2006; Carta, 2015). Finally, we built a data matrix (418 beech stands × 6 environmental variables) which was subjected to cluster analysis under Euclidean Distance and UPGMA agglomeration method.

We applied ANOVA to each bioclimatic variable and elevation for testing differences among clusters. Only p values ≤ 0.01 were considered significant. Statistical analyses were carried out with PAST v. 3.15 (Hammer *et al.*, 2001; Hammer, 2017) and R 3.3.1 (2016) software.

Results

Multivariate analysis distinguished two main clusters with a dissimilarity index of 0.35 (Fig. 2). Cluster "A" included about 65% of putatively heterotopic populations (75 out of the 113 found in the literature) and seven control points (82 points in total). Cluster "B" included most control points (298 out of 305) and 38 points (i.e., populations) taken from literature (Tab. 1). ANOVA (Tab. 2, Fig. 3) highlighted that cluster A included all the populations located at an altitude ≤ 600 m a.s.l., whereas cluster B those at higher elevation (> 600 m a.s.l.). Cluster A was further characterized by stands with a mean annual temperature significantly higher than those of cluster B (t-test, difference between means = 4.1 °C), as well as higher values of continentality (t-test, difference between means = 1.6 °C) and lower values of annual precipitation (t-test, difference between means = 72.8 mm). No significant differences in seasonality of temperature and precipitation were found between clusters.

Discussion

The two clusters obtained by the multivariate analysis are statistically supported by four out of six variables, as highlighted by univariate analyses. In the light of this result, we define as 'quantitatively heterotopic' the populations included in cluster A and 'normotopic' (a new term) those included in cluster B.

Altitude was the most discriminating variable, which is in accordance with the concept of heterotopy used by previous authors in Italy (Pignatti, 1994). Based on our results, populations located at an altitude less than 600 m a.s.l. could be recognized as quantitatively heterotopic. This altitudinal limit is slightly higher than the threshold of 500 m a.s.l. used by Sabbatini *et al.* (2011) to define the "abyssal" extra-zonal beech forests.

About 65% of the Italian beech populations previously mentioned as 'heterotopic' are situated below 600 m a.s.l.

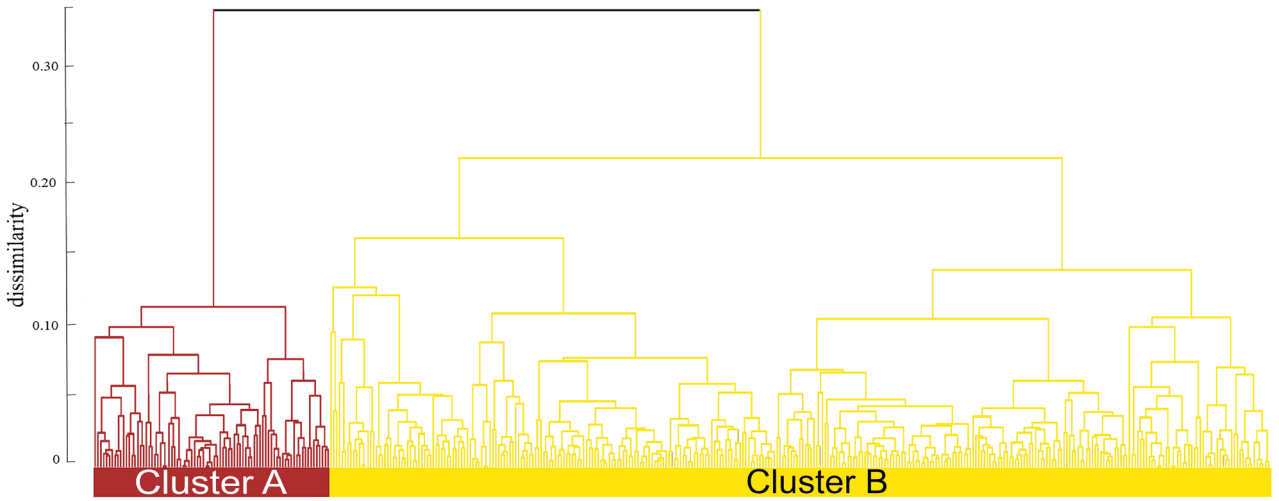

Figure 2. Cluster analysis of 418 beech stands (113 putatively heterotopic + 305 control points based on vegetation series) based on elevation and five bioclimatic variables.

Table 2. Comparison of altitude and climatic parameters between clusters A and B obtained by the multivariate analysis. Only variable marked with the asterisk were significantly different ($p < 0.01$).

	A		B	
	Min-Max	**μ (± SD)**	**Min-Max**	**μ (± SD)**
Altitude (m a.s.l.)*	155–600	450.6 (± 88.92)	605–1992	1124.9 (± 275.8)
Mean temperature (°C)*	11.7–15	13.3 (± 0.7)	4.4–13.4	9.3 (± 1.7)
Temperature seasonality	541.6–660.9	610.9 (± 21.7)	545.1–656.8	615.9 (± 19.9)
Continentality (°C)*	22.2–29.7	25.6 (± 1.4)	21–28.9	24 (± 1.3)
Annual precipitation (mm)*	527–936	753.3 (± 103.1)	520–1022	826.2 (± 104.7)
Precipitation seasonality	15–54	28.1 (± 6.3)	16–54	26.8 (± 7.9)

Interestingly, they comprise three populations contained within the polygons of potential natural vegetation with *Fagus sylvatica,* namely those of Mt. Foligno (Montelucci, 1956) and Passo Broscione (Anzalone, 1961a) in the Latium region and that of Vallone Grande in Gargano massif (Hoffman, 1961). On the other hand, 38 beech populations previously defined as 'heterotopic', like e.g. Mt. Cetona and Pietraporciana (Siena, Tuscany), Mt. Penna (Grosseto, Tuscany) and Mt. Spigno (Foggia, Puglia), should be considered as normotopic in the light of our results.

The annual mean temperature is the second best discriminating variable between heterotopic and normotopic clusters, confirming that this climatic factor is highly associated with altitude (Körner, 2007).

With the notable exception of the populations on the Gargano massif (Puglia) and in the Marche, the quantitatively heterotopic populations are located on the Tyrrhenian side (mostly in Tuscany and Latium). The seven control points falling in the heterotopic cluster follow the same distribution pattern: one is located in Gargano, one at the boundary between Marche and Umbria, four in Lazio, and one in southern Tuscany. This pattern was apparent also in the 'putatively heterotopic' populations sourced from extant literature, as clearly shown in Fig. 1.

Although annual precipitations in the areas holding quantitatively heterotopic populations are lower than those recorded in areas where normotopic ones are found, the longitudinal pattern might be related to the humid bioclimate of the western side of the Italian peninsula (Rivas-Martinez *et al.*, 2011). This feature is known to have favored the persistence of relicts at the easternmost boundary of their range, like the isolated populations of *Vandenboschia speciosa* (Willd.) G.Kunkel (Ferrarini, 1977), *Woodwardia radicans* (L.)

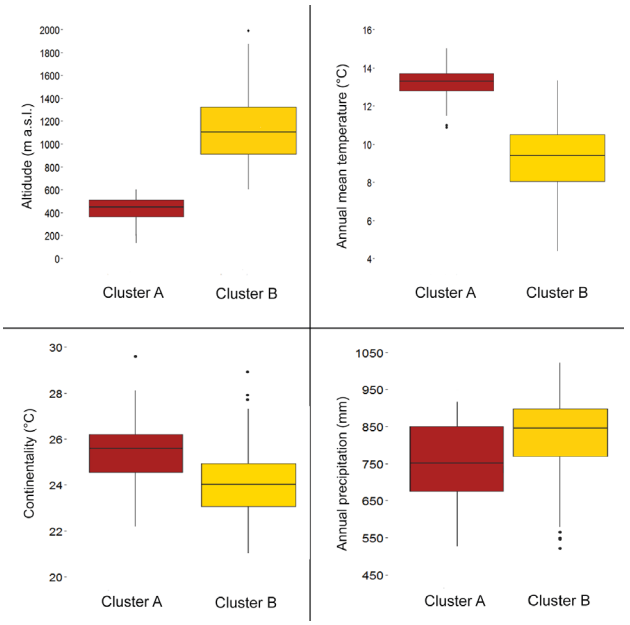

Figure 3. Boxplots of the environmental variables that were significantly different ($p < 0.01$) between the two clusters. Circles represent outlier values.

Sm. (Caputo & De Luca, 1970; Gramuglio *et al.*, 1982) and *Hypericum elodes* L. (Corti, 1956; Carta, 2015; Carta *et al.*, 2015).

At low altitudes, the high level of humidity associated with favourable local microclimatic factors, such as deep and fertile soils (Di Filippo *et al.*, 2012), compensates for the higher temperatures (Scoppola & Caporali, 1998; Innangi *et al.*, 2015), which are known to affect negatively the productivity and growth of beeches (Jump *et al.*, 2006; Piovesan *et al.*, 2008).

The southernmost Italian populations are located in Sicily. Although markedly thermophilous from a phytosociological point of view (Abbate *et al.*, 2003), they were never reported as heterotopic. Indeed, the lowest altitude recorded for beech in Sicily is 800 m a.s.l. on the eastern slope of Mount Etna (Cullotta *et al.*, 2015), which according to our results defines those populations as normotopic.

In their study on beech populations in Northern Europe, Fang & Lechowic (2006) highlighted a mean temperature annual range, annual mean temperature, and annual mean precipitation of 19.6 °C, 6.6 °C, and 1272.3 mm, respectively. North European populations thus benefit from a higher annual mean precipitation

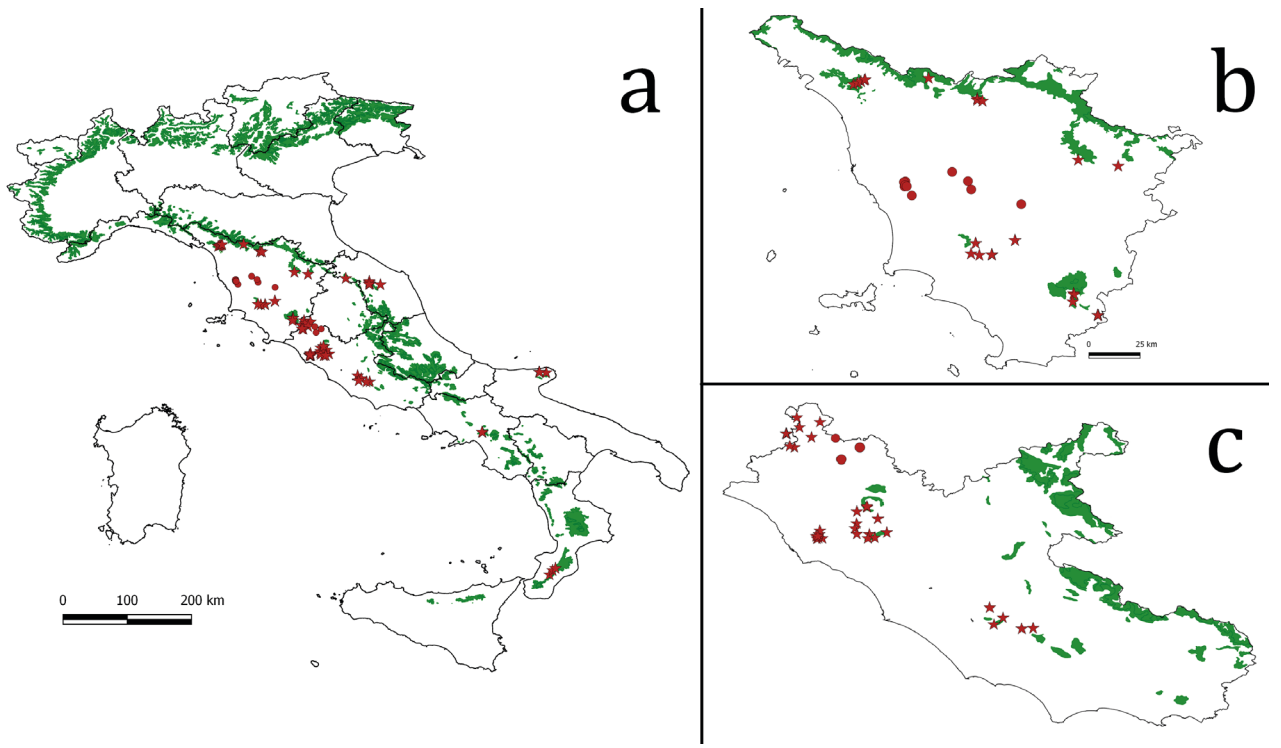

Figure 4. Distribution of the heterotopic beech populations found in our study. Stars represent populations included in the *Fagus sylvatica* vegetation series or within 20 km of distance. Circles represent the populations distant more than 20 km from natural vegetation series with European beech (represented in green). A close-up on Tuscany (b) and Lazio (c), the two regions richest in quantitatively heterotopic stands, is shown.

and lower temperatures with respect to the Italian populations. Therefore, Italian populations, and particularly the heterotopic ones, could be affected by climate change earlier than those at higher latitudes (Innangi *et al*., 2015). In this framework, a clear definition of heterotopy is useful to set up monitoring plans and genetic studies, as well as floristic, phytosociological and biogeographic researches.

Most of the quantitavely heterotopic populations are located outside of vegetation series with European beech and, among these, some are distant more than 20 km (Fig. 4). These peculiar populations could be interpreted not only as heterotopic, but also as biogeographical-ecological relicts (Aubréville, 1970).

In conclusion, our results led us to define as 'quantitatively heterotopic' in Italy those beech populations located at an altitude ≤ 600 m a.s.l., and with a mean annual temperature generally higher than 12 °C. The method used here to define *ad hoc* thresholds (if any) for heterotopy quantification could be easily applied to other species.

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