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NICHE HETEROGENEITY AND OLD-GROWTH FORESTS CONSERVATION VALUE

Vascular plants understorey of an old-growth beech forest was compared to a managed stand, similar for biogeographical, climatic and abiotic features. Parametric tests and accumulation and rarefaction curves were used to compare the stands in terms of vascular plant diversity at stand level and among sampling units.

The sampled understorey species were characterized in terms of functional traits and Ellenberg's indicator values; next, we calculated four different pairwise plot-to-plot dissimilarity matrices based on: 1. species presence/absence, 2. cover values, 3. functional traits and 4. Ellenberg's indices. We applied a permutational multivariate extension of ANOVA to test whether the forest stands significantly differ in the considered features. Furthermore we used fourth corner analysis to highlight which single functional trait is significantly associated to each stand.

Although not richer at plot level the old-growth stand resulted more diverse both at stand level and in terms of among-plots diversity than the managed one. All the comparisons performed through permutational multivariate ANOVA showed significant differences, with the exception of the one based on Ellenberg's indices.

From a functional and ecological perspective in the old-growth forest we noted: 1. a relative increase of hemicryptophyte species with limited dispersal abilities (ant-dispersed or non specialized); 2. a decrease in early-flowering geophytes; 3. a parallel increment in small seeded, wind-dispersed species adapted to relatively open and bright conditions (gaps).

Our results suggest that in the old-growth stand the high vertical and horizontal structural heterogeneity of the canopy modulates the ecological conditions at the forest floor and increases the environmental heterogeneity. This mechanism is likely to allow the coexistence of a higher number of species, with different ecological requirements.

Key words: old-growth forest; rarefaction curves; forest management; functional traits; permutational multivariate analysis of variance.

Parole chiave: foreste vetuste; curve di rarefazione; gestione forestale; caratteri funzionali; analisi multivariata permutazionale della varianza.

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1. INTRODUCTION

Italian forests are the result of age-long coevolution of ecological and social-economic issues. Cultivation and management as means to economic ends have deeply modified their structure and composition, reducing complexity and diversity (CIANCIO, 2007).

In Italy, natural disturbance regime of forest ecosystems has been almost everywhere altered by anthropogenic activities (MOTTA, 2002) even if with different intensities depending on local conditions, of both environmental and socio-economic nature. Despite the fact that Italian landscapes have been modified for millennia, there are remote mountain areas where it is possible to find patches of old-growth forests (PIOVESAN *et al.*, 2005), i.e. those forests developed during long periods without relevant human impact and natural catastrophic disturbances (PETERKEN, 1996). Likely, these stands escaped intensive logging due to their inaccessibility or unique historical contingencies.

Lately, the interest of Italian researchers for these ecosystems has grown (PIOVESAN *et al.*, 2005; GIANNINI and SUSMEL, 2006; BURRASCANO *et al.*, 2008), also thanks to the attention raised by international conventions and agreements on the subject (e.g. Pan-European Biological and Landscape Diversity Strategy, European Strategy for Plant Conservation).

Old-growth forests are characterized both by high levels of structural heterogeneity (NILSSON *et al.*, 1995; NORDEN and APPELQVIST, 2001) and biological diversity (FRANKLIN and SPIES, 1991; SIITONEN *et al.*, 2002). For this reason they are an important reference point when evaluating human impact on forest ecosystems (PETERKEN, 1996), within the global view of achieving a Sustainable Forest Management which integrates ecological, social and economic objectives (UNCED, 1992; CIANCIO, 2002; FAO, 2005).

The aim of our research is to give a contribution to the knowledge of Italian old-growth forests. We studied the understorey vascular plant composition of Fonte Novello beech stand, in “Gran Sasso e Monti della Laga” national park (BLASI, 2008) through a comparison with a managed beech stand. We chose a comparative approach to achieve insights on the effect of forest management on plant biological diversity. We analyzed the differences between the stands considering not only the variations in species richness and composition, but also functional traits and Ellenberg's indicator values, in fact ecological differences are believed to be reflected in each of these features.

2. METHODS

2.1. Study area

The beech forest of Fonte Novello is located inside the Gran Sasso e Monti della Laga national park, close to the boundary between the municipalities of Pietracamela and Fano Adriano (TE). This forest ranges from 1275 to 1450 m a.s.l. and is located on the northern slope of Monte Corvo (2623 m), on the left bank of the mountain stream Fosso Venacquaro. This stand encompasses 18.8 ha and is composed by a mosaic of small patches belonging to different phases of stand structural development. The height of the canopy is comprised between 25 and 30 m, witnessing good site fertility. Trees older than 400 years have been reported (CIAPANNA and ETTORRE, 2003).

The stand is mainly monospecific with few individual of *Acer pseudoplatanus* and *Salix caprea*. The density of stems with diameter at breast height larger than 2.5 cm is 1063 per hectare, basal area is 51 m²/ha. Estimated growing stock is over 600 m³/ha (BLASI, 2008).

The comparison beech forest of Tassete - Grotta delle Fosse is a high forest located on the eastern slope of Monte Cima Alta, at the head of Rio San Giacomo valley. This area was chosen for its similarity and closeness (5.6 km) to Fonte Novello stand.

Both the stands are *Fagus sylvatica* pure stands with few clustered individuals of *Taxus baccata* and *Ilex aquifolium* in the dominated layer; they are within the same altitude range, have the same prevalent aspect (eastern) and are on bedrock that consists of alternations between arenaceous-marls and organogenic limestones locally covered by olocenic detritic deposits. The two stands share the same bioclimatic, geologic and morphologic characteristics; on the basis of the hierarchical classification approach proposed by BLASI *et al.* (2000), they thus refer to the same potential natural vegetation (BLASI *et al.*, 2005; BURRASCANO *et al.*, 2009). For these reasons, differences detected between stands are likely to be due to past management.

According to the phytosociological relevés performed during this study, both stands can be referred to the association *Cardamino kitaibelii-Fagetum sylvaticae* (*Aremonio-Fagion*). This association includes the neutro-basiphilous beech woods located at the highest altitudes in the central and northern Apennines.

The annual average temperature registered at the meteorological station of Pietracamela (1000 m a.s.l.) is 10.6 °C. Average annual precipitation is 1062 mm. On the basis of these data, the meteorological station of Pietracamela is located in the temperate region with an oceanic bioclimate, thermotype is inferior supratemperate and ombrotype is inferior humid (BLASI, 2007).

2.2. Beech forests in central Apennine - the case of Fonte Novello

According to the National Forest Inventory (INFC, 2007), the total area covered by beech in Italy is more than 1 million hectares; about 122 thousand hectares are in the Abruzzo region. Respectively 1,493 and 1,378 ha of beech high forest belong to the municipalities of Pietracamela and Fano Adriano (GABBRIELLI, 2004).

The uniform shelterwood system has been systematically prescribed for beech Apennine high forests on public properties. However, in central Apennine, NOCENTINI (2009) noted a separation between “scientific forestry” and real life management as only rarely the shelterwood system has been applied thoroughly. Generally, a very intensive logging at rotation age utilizes 50% or more of standing volume, instead of 30% as prescribed; removal cuttings are usually indefinitely postponed because they are not considered financially profitable (CIANCIO *et al.*, 2008).

The forests and grasslands of Pietracamela and Fano Adriano underwent a destiny partially different; they have been managed, probably since 1388, by independent authorities (PERRI and PERRI, 2001). In 1826 the approval by the Kingdom of Two Sicilies of the so called Bourbon Law dictated that all public owned forests be managed according to “regular felling”, i.e. clear cut leaving 58 seed trees per hectare. As this law absolutely prohibited grazing in the cut section, it was firmly contested by the local community and after 1877 the traditional management system in the area became the “taglio a salto” i.e. selective cut maintaining a minimum distance between remaining trees of at least 5 m (GABBRIELLI, 2004).

The stand of Fonte Novello did not undergo intense cutting since 1600 (GABBRIELLI, 2004). The municipalities of Pietracamela (founded in 1808) and Fano Adriano separated in 1816 and this stand, located at the boundary between the two municipalities, was long contended. This dispute, (not yet resolved nowadays), saved the stand by being intensively exploited. In 1868 Fonte Novello was the last high forest of the area. Probably during the World War 2 the stand was subjected to partial logging. Later on, an intense emigration depopulated the villages of Pietracamela and Fano Adriano thus grazing and cuttings drastically diminished, favoring a slow recover of the stand (GABBRIELLI, 2004). In 1991 the area became part of the “Gran Sasso e Monti della Laga” national park.

2.3. Sampling design

Using *ArcGis* 9.2 we excluded from the study areas a 20-m wide buffer area to minimize the edge effect, and then we superimposed a 20 x 20 m grid. We randomly selected ten 400 m² plots in each stand. For each plot we recorded site characteristics (elevation, aspect, slope, substrate,

physiognomy) and the complete list of vascular plant species within each subplot, registering their cover using the Braun-Blanquet 7-degrees ordinal scale (r, +, 1, 2, 3, 4, 5; BRAUN-BLANQUET, 1932). We divided the plot in four 100 m² subplots to reduce the possible bias due to the subjective estimation of plant cover.

The survey took place from 19 June to 4 July 2008. Nomenclature follows CONTI *et al.* (2005).

2.4. *Vascular plants species richness*

Species Richness is the simplest way to measure the biological diversity of a community (α -diversity) or region (γ -diversity), (MAGURRAN, 1988) and is still the most common index ecologists use to describe a community. A major problem in the use of species richness is that, as more individuals are sampled, more species will be recorded. The sampling curve rises relatively rapidly at first, and then much more slowly in later samples as increasingly rarer taxa are added until it should eventually reach an asymptote (GOTELLI and COLWELL, 2001).

An accumulation curve graphs the total number of species sampled, as sample units are progressively added. A rarefaction curve, instead, is produced by repeatedly re-sampling the pool of N samples, at random, plotting the average number of species represented by 1, 2, ..., N samples. Thus, rarefaction curves generate the expected number of species in a small collection of n samples drawn at random from the large pool of N samples (GOTELLI and COLWELL, 2001).

Richness increases in an asymptotic way as sampling units are added. Accumulation and rarefaction curves, thus, allow controlling for sampling intensity when making a comparison between communities. Species richness values of the understorey vascular plant of the two stands have thus been compared using two different approaches.

Firstly, plot richness values of the two stands have been compared using a two-tailed t-test. Normality and homoscedasticity of data were assessed using respectively Lilliefors' distance test and F-test.

Secondly, we followed the approach of GOTELLI and COLWELL (2001) using the software *EstimateS* (COLWELL, 2006) to build accumulation and rarefaction curves.

2.5. *Functional diversity*

Functional diversity was defined by TILMAN (2001) as "those components of biodiversity that influence how an ecosystem operates or functions". It has been seen as the key for understanding the influence of

community composition on ecosystem processes, such as productivity, nutrient cycling, carbon sequestration or stability to perturbations (PETCHEY and GASTON, 2006). The underlying assumption is that the most important processes in an ecosystem are the product of those operating at the level of the populations that compose it, while these processes are the consequence of the species traits (AUBIN *et al.*, 2009).

LAVOREL *et al.* 2007 defined a functional trait as any morphological, ecophysiological, biochemical, demographical or phenomenological characteristic of a species that, on the one hand, affects the way the species respond to environmental changes and on the other hand modulates the effects that plants have on ecosystem functions.

We selected nine widely used functional traits (Table 1) mostly related to two fundamental challenges plants have to face to thrive: competition for light and dispersal and colonization ability. The first group (life form, growth form, height) is related to the vertical profile of leaf area and light attenuation. Species with canopies at different depths in this profile are operating at different light incomes, heat loads, wind speeds, humidities, and with different capital costs for supporting leaves and lifting water to the leaves (GIVNISH, 1995; WEIHER *et al.*, 1999). The attributes related to reproduction and dispersion (dispersal modality, seed persistence in the seed bank, seed size, seed shape, flowering time and span) are among the most important

Table 1 – Description of the plant functional traits used in this study.

<i>Functional Trait</i>	<i>Data Type</i>	<i>Attribute</i>
Life Form	Nominal	Chamaephyte; hemicryptophyte; geophyte; therophyte; phanerophyte, nanophanerophyte
Growth form	Nominal	Bulbous, Caespitose, Lianose, Reptant, Rhizomatous, Rosulate, Scapose, Succulent
Dispersal mode	Nominal	Wind, Ingested, Adhesive, Ant, Autochorous, Diszoochorous, Non-specialized
Seed persistence in soil	Binomial	Persistent; non persistent
Maximum height	Ordinal	(1) <20 cm; (2) 20-50 cm; (3) 50-100 cm; (4) >100 cm
Propagule size (Length)	Ordinal	(1) < 0.5 mm; (2) 0.5-2.0 mm; (3) 2.1-5.0 mm; (4) 5.1-10.0 mm; (5) > 10 mm
Propagule shape (length/width ratio)	Ordinal	(1) < 1.5; (2) 1.6-2.5; (3) > 2.5
Start of flowering season	Quantitative	Month
Length of flowering season	Quantitative	# of months

factors for the maintenance of local species diversity in old-growth forests (NILSSON *et al.*, 1995; NORDEN and APPELQVIST, 2001; RICOTTA *et al.*, 2010). Beside the functional traits listed above, we compared the two stands also on the basis of the ecological needs of the understorey species as witnessed by Ellenberg indicator values (ELLENBERG, 1974; PIGNATTI, 2005). We took into account the indices related to light, humidity, pH and nutrients, as these indices are the ones most relevant at a local scale (DUPRÉ, 2000).

2.6. *Multivariate analysis*

We used the approach proposed by RICOTTA and BURRASCANO (2008) and then applied by BURRASCANO *et al.* (2009) to evaluate the existence of meaningful differences in the overall plant species composition between the old-growth and the managed beech forest.

We calculated 4 dissimilarity matrices for all 20 plots sampled in both stands. These matrices are based on pairwise plot-to-plot differences in species composition (1. presence-absence and 2. cover), 3. functional characters and 4. Ellenberg's indices, respectively. Pairwise plot-to-plot differences in species composition were computed using Jaccard dissimilarity on species presence and absence scores and Bray-Curtis on species coverage (see PODANI, 2001). Plot-to-plot dissimilarity in terms of functional traits and Ellenberg's indicators were computed using the formula proposed by IZSAK and PRICE (2001), based on pairwise species dissimilarities calculated using Gower's (1971) formula modified by (PODANI, 1999). This formula applies to a mixture of different measurement scales (i.e. categorical, ordinal and ratio-scale variables) and allows missing data. It is therefore particularly adequate for calculating dissimilarities based on species functional traits. For mathematical details see PODANI and SCHMERA (2006).

Based on the above pairwise plot-to-plot dissimilarity matrices, we applied a permutational multivariate extension of traditional analysis of variance (PERMANOVA, ANDERSON, 2001) to test whether both forest stands significantly differ in their species composition, functional characters and Ellenberg's indices.

PERMANOVA was performed separately for the four plot-to-plot dissimilarity matrices with the software PERMANOVA (ANDERSON, 2005) freely available at: <http://www.stat.auckland.ac.nz/~mja/Programs.htm>; PERMANOVA analysis was limited to understorey species.

After testing for difference in the overall species composition of the two stands, we evaluated the existence of significant associations between each single functional trait and the management system applying the fourth corner analysis (DRAY and LEGENDRE, 2008). This is a 'direct' approach to relate plant traits to environmental variables by simultaneously analyzing three

matrices (1. presence-absence of species by plot, 2. species by functional traits and 3. plot by management system).

3. RESULTS

We recorded a total of 98 vascular plant species. Species richness at stand level was higher in the old-growth stand than in the managed one (78 vs 67 species). We found 47 species common to both stands; 31 species were found exclusively in Fonte Novello forest while 20 species were found exclusively in the comparison area.

Average plot species richness with 95% confidence interval was 27.1 ± 5.6 sp/plot for the old-growth stand and 27.9 ± 5.0 sp/plot for the managed one. Standard deviations were respectively 7.38 and 6.65. Data were normally distributed and homoschedastic; no significant difference resulted between the average plot richness of the two stands ($t_{18}=0.24$; $p=0.80$).

Accumulation curves (Fig. 1; solid line) have, as expected, an irregular shape and show two cross-overs (4th and 6th sampling unit). Rarefaction curves show an asymptotic shape even if none of them look to have satisfactorily reached the asymptote.

Three out of four comparisons performed through PERMANOVA showed the existence of significant differences between the two stands. The two stands resulted significantly different in terms of understorey com-

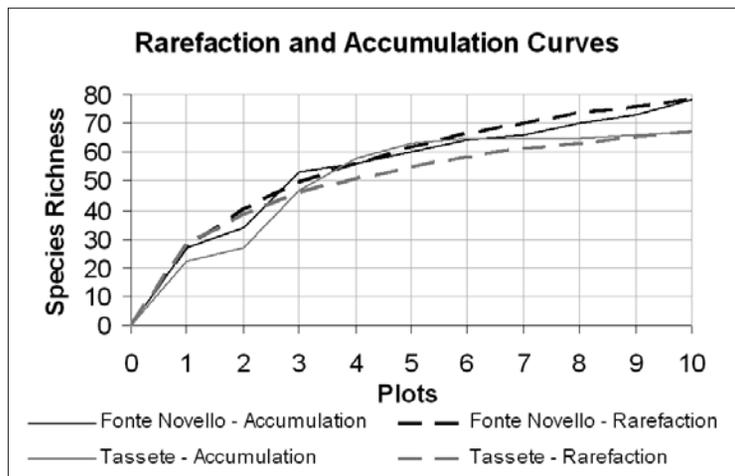


Figure 1 – Accumulation (solid line) and Rarefaction (dashed line) curves of plant species richness in the two sampled stands (black-old-growth; gray-comparison).

position (presence-absence: $F_{1,18} = 2.5304$, $P < 0.001$; cover data: $F_{1,18} = 2.8173$, $p < 0.001$) and functional diversity ($F_{1,18} = 3.7350$; $p < 0,001$).

After the fourth corner analysis some interesting trends have been observed (Fig. 2, Fig. 3): in the old-growth stand we observed a significant increase in hemicryptophytes and in species with scapose growth form, especially phanaerophytes while the managed stand resulted richer in rhizomatous geophytes. Fonte Novello resulted also richer in species with small, persistent seeds; although not significant we noticed an increase in the number of species dispersed by adhesion (epizoochory) or wind (Fig. 2). The managed stand resulted instead significantly richer in species dispersed either by ingestion or by diszoochory.

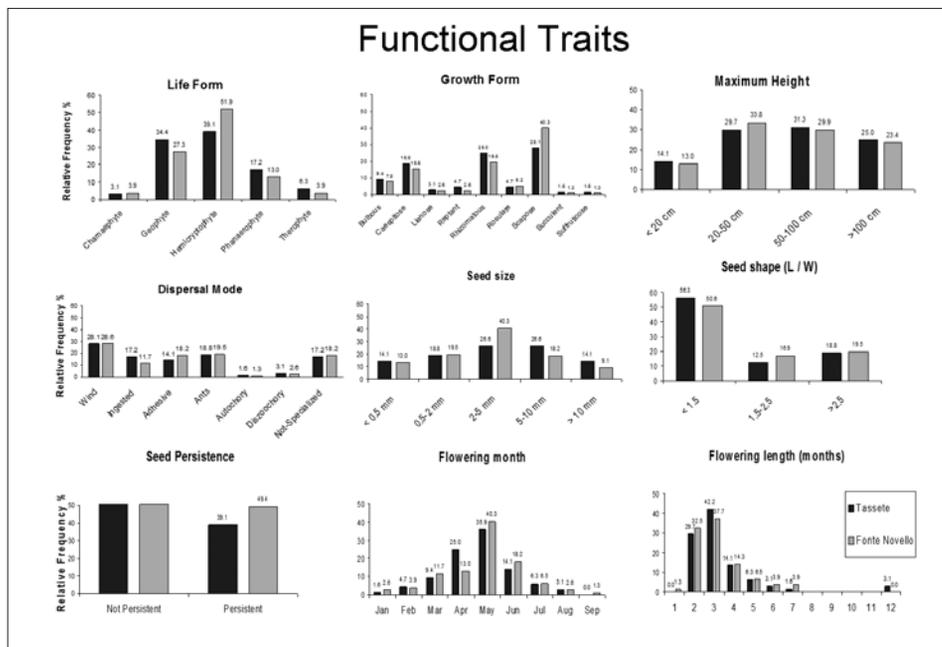


Figure 2 – Relative distribution of the attributes of different plant functional traits in the old-growth stand (Fonte Novello) and in the comparison area (Tassete).

In terms of Ellenberg indicator values the two stands do not show significant differences ($F_{1,18} = 0.3268$; $p > 0.7$). Although not significant, a slightly lower proportion of species in the old-growth stand appear to be adapted to low-light conditions (Fig. 4). We also observed a slight increase in species adapted to soil conditions either very rich or very poor of nutrients while most of the species of the managed stand are associated to intermediate conditions.

	Managed	Old-growth
Chamaephyte		
Geophyte		
Hemicryptophyte		
Phanaerophyte		
Therophyte		
Bulbos		
Caespitose		
Lianose		
Nanophanaerophyte		
Reptant		
Rhizomatous		
Rosulate		
Scapose		
Succulent		
Suffruticose		
Wind		
Self_Dispersed		
Diszoochory		
Ingested		
Adhesive		
Ant-dispersed		
non_specialized		
Seed Persistence		
Height		
Propagule dimension		
Flowering_starting		
Flowering_last		

Figure 3 – Results of the Fourth Corner Analysis. Black cells indicate significant ($p < 0.05$) positive associations between the frequency of a functional trait and the management system. Gray cells indicate significant negative associations. White cells indicate no significant association.

4. DISCUSSION

The old-growth stand is richer of plant species than the managed one; this feature is not due to a difference in plot-level diversity. The rarefaction curves show a higher level of richness at stand level in the old-growth forest. This seems to be due to a higher among-plot differences probably related to a higher heterogeneity of environmental conditions. The plot-to-plot comparison based on the Ellenberg indicator values showed a shift toward conditions brighter and more heterogeneous in terms of soil nutrients even if it did not show significant differences; this may be due either to the weak performance of the Gower dissimilarity index in case of a great amount of ties in the species-by-traits matrix (as Ellenberg indicator values are measured on an ordinal scale) or to the high level of ecological overlap between species in different plots that resulted in a low pairwise plot-to-plot functional

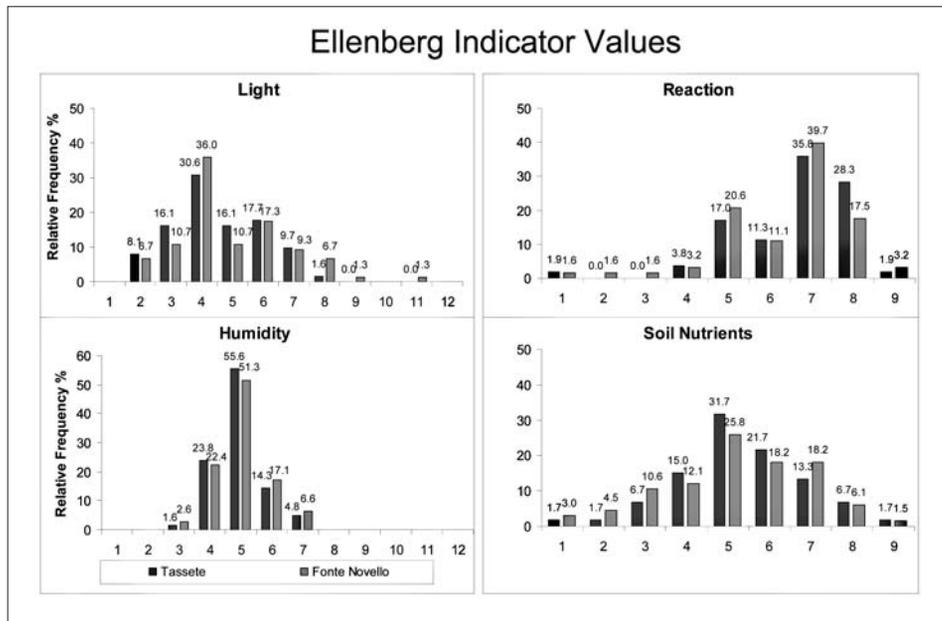


Figure 4 – Relative distribution of Ellenberg indicator values in the old-growth stand (Fonte Novello) and in the comparison area (Tassete).

dissimilarity. WHITTAKER (1972) suggested that a pairwise dissimilarity matrix among a set of plots is in itself an expression of the beta diversity of that set; however the approach used in this paper only tests for differences in the position of sets in multivariate space of ecological or functional characters but does not give any indication on the variability associated to each treatment (ANDERSON *et al.*, 2006). For a promising way to make a direct comparison in terms of β -diversity based on pairwise dissimilarity matrix see ANDERSON *et al.* (2006) and RICOTTA and BURRASCANO (2009).

The difference observed regarding species functional traits of the species highlights two main features. The first one concerns light availability at forest floor. Beech forest canopy is usually associated with intense shading at ground level. Understorey species are usually adapted to low-light intensity either physiologically (shade-tolerance) or phenologically (shade-avoidance). Indeed, many species typical of beech forests are usually geophytes with underground storage organs that make them able to accomplish most part of their vital cycle in spring, before beech leaf out. In the old-growth forest we observed a relative decrease of early-flowering geophytes in favour of hemicryptophytes flowering in early or late summer. Moreover we observed an increase in wind-dispersed, small-seeded species adapted to bright

conditions (e.g. *Silene nutans*, *Campanula scheuchzeri* subsp. *pseudostenocodon*, *Equisetum arvense*). These species are probably associated with a high proportion of gaps in the canopy.

The second feature observed regards understorey species with poor dispersal capabilities exclusively found in Fonte Novello forest. Some of them (*Luzula forsteri*, *L. sylvatica*, *Carex sylvatica*, *Stellaria nemorum*) have already been pointed out by HERMY *et al.* (1999) as associated to stands with a long ecological continuity (NORDEN and APPELQVIST, 2001). Forest interior species ant or ballistically dispersed are likely to be strongly affected by intensive management and, after a local extinction, may be very slow or unable to recolonize a forest patch (DUFFY and MEIER, 1992).

Concluding, the high vertical and horizontal structural heterogeneity of the studied old-growth stand modulates the ecological factors the species of the understorey have to face. As the environmental heterogeneity increases, species with different ecological requirements are able to coexist in a fine-grained mosaic of microhabitat, in accordance with the niche diversification hypothesis (CONNELL, 1978).

RIASSUNTO

Eterogeneità ambientale e valore conservazionistico delle foreste vetuste

La flora vascolare del sottobosco di una faggeta vetusta è stata confrontata con quella di un bosco gestito, simile per caratteristiche biogeografiche, climatiche e abiotiche. Test parametrici e curve di accumulazione e di rarefazione sono stati usati per confrontare i due boschi in termini di diversità di flora vascolare a livello di bosco e di unità di campionamento.

Le specie del sottobosco rilevate sono state caratterizzate in termini di caratteri funzionali e indici di Ellenberg; inoltre, abbiamo calcolato quattro diverse matrici di dissimilarità tra le unità di campionamento basate su: 1. presenza/assenza delle specie, 2. valori di copertura, 3. caratteri funzionali e 4. indici di Ellenberg. Abbiamo applicato un'ANOVA multivariata permutazionale per verificare la presenza di differenze significative tra i due boschi nelle caratteristiche considerate. Inoltre abbiamo usato la *fourth corner analysis* per evidenziare quali caratteri presi individualmente sono significativamente associati a ciascun bosco.

Nonostante non sia più ricco in numero medio di specie per unità di campionamento, il bosco vetusto risulta più diverso di quello gestito sia in termini di diversità tra i plot che considerando l'intero bosco. Tutti i confronti effettuati tramite l'ANOVA multivariata permutazionale hanno dimostrato differenze significative, eccetto nel caso degli indici di Ellenberg.

Da un punto di vista funzionale ed ecologico nel bosco vetusto abbiamo notato: 1. un aumento relativo di emicriptofite con capacità di dispersione limitata (mirmecocore o non specializzate); 2. una diminuzione nelle geofite vernali; 3. un incremento di specie a semi piccoli dispersi dal vento adattate a condizioni relativamente aperte e luminose (aperture della volta arborea).

I nostri risultati suggeriscono che nel bosco vetusto l'elevata eterogeneità strutturale verticale ed orizzontale della volta arborea modula le condizioni ecologiche al suolo aumentando l'eterogeneità ambientale. Questo meccanismo potrebbe essere alla base della coesistenza di un numero elevato di specie con differenti esigenze ecologiche.

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